

# PHILOSOPHICAL TRANSACTIONS.

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- I. *On the Organization of the Fossil Plants of the Coal-measures.*—Part VII. *Myelopteris, Psaronius, and Kaloxylon.* By W. C. WILLIAMSON, F.R.S., Professor of Natural History in the Owens College, Manchester.

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THE existence or non-existence of the remains of Palms in the Carboniferous strata has long been a debated geological question. Accepting the determinations of CORDA as announced in his ‘Flora der Vorwelt,’ many geologists admitted these true endogens into their lists of Carboniferous plants. COTTA had figured, in his ‘Dendrolithen,’ three very anomalous stems, under the names of *Medullosa porosa*, *stellata*, and *elegans*. CORDA, in his ‘Flora der Vorwelt,’ subsequently figured two stems from Carboniferous strata obviously allied to one, at least, of COTTA’s types, under the names of *Palmacites carbonigerus* and *P. leptoxylon*, which he placed in the class of Palms. COTTA’s figures of *Medullosa elegans* are very misleading, though they are not very unlike the specimens which he probably described. Some specimens now in the British Museum which came direct from COTTA, and for having my attention drawn to which I am indebted to my friend Mr. CARRUTHERS, exhibit a remarkable areolation when cut transversely. This areolation COTTA has not only copied but exaggerated; hence the peculiar aspects of his figures 1 & 8 of his *Medullosa elegans*; it certainly is not a constant and normal feature, but the result of some change produced subsequent to the life of the plant—most probably a consequence of partial desiccation of the stem. COTTA’s drawings of the cortical layer also are very misleading; hence it is very unsafe to accept his delineations apart from the study of his specimens, some of which, I fear, are no longer to be found. The consequence is that two of his species, *M. stellata* and *M. porosa*, remain too obscure to be relied upon without further evidence than COTTA has handed down to us.

The first to throw doubt upon the Monocotyledonous character of these plants was M. BRONGNIART in his ‘Tableau des genres de Végétaux fossiles,’ published in 1849, extracted from the ‘Dictionnaire Universel d’Histoire Naturelle.’ He identified COTTA’s *Medullosa elegans* with some important plants not uncommon in the Carboniferous beds

of Autun; and whilst he thought that these specimens displayed a structure analogous to that of some Monocotyledons, especially of *Dracæna*, he adds, "il y ait des différences fort essentielles et qui rendent très-difficile d'établir des rapports entre ces fossiles et les végétaux vivants"\*. M. BRONGNIART consequently proposed to make COTTA's *Medullosa elegans* the type of a distinct genus under the name of *Myeloxylon*. At a later page of his work (p. 97) he further gives a list of fourteen Carboniferous Monocotyledons, in which he includes seven species of *Trigonocarpum*, his proposed genus *Myeloxylon*, and the *Palmacites carbonigerus* and *leptoxylon* of CORDA, at the same time declaring that all these supposed Carboniferous Monocotyledons are "très-douteuses et imparfaitement connues." At p. 89 of his work he retains CORDA's genus *Palmacites*, but remarks respecting the two species from the Carboniferous strata, viz. *P. carbonigerus* and *leptoxylon*, that they appear to be distinct from the Palms, and probably also from the group of Monocotyledons, thinking them analogous to the *Medullosa elegans* of COTTA, adding, in reference to the latter plant, "qui n'est certainement pas un palmier."

In 1864 GOEPPERT referred to the *Medullosa elegans* under the name of *Stenzelia elegans*, separating it from COTTA's other species†, and regarding it as a generalized type of vegetable organization combining characters which are to be found separated in *Dracæna*, in Ferns, and in some Gymnospermous stems.

In January 1872 Mr. BINNEY made a very brief reference to *Medullosa elegans* in a communication to the Literary and Philosophical Society of Manchester, in which he says that "from some specimens in his cabinet he is led to believe that COTTA's *Medullosa elegans* is merely the rachis of a Fern or a plant allied to one"‡. The context shows that Mr. BINNEY had obtained specimens of the plant from the Carboniferous strata of Oldham.

In September 1873 I made a communication to the Botanical Section of the British Association for the Advancement of Science at their Meeting at Bradford, where I directed special attention to the organization of this plant, and announced my conviction that it was not only a Fern, but that it belonged to the aberrant group of the Marattiaceæ.

On January 26, 1874, my indefatigable fellow-labourer in the field of palæophytology, Professor RENAULT, presented to the Académie des Sciences of Paris another of his very important series of memoirs, entitled "Recherches sur les végétaux silicifiés d'Autun;" this last of which he designates "Étude du genre *Myelopteris*." Under this generic name he comprehends the *Medullosa elegans*, with its various synonyms of *Medullosa*, *Stenzelia*, and *Myeloxylon*. He assigns his reason for adopting the new name in the abstract of his memoir (which alone has yet been published) in the 'Comptes Rendus' of the above date:—"Pour conserver le nom, premier en date, donné par M. BRONGNIART à ces portions de plantes, et en même temps pour rappeler leur nature, je les désignerai sous le nom de *Myelopteris*." The reason thus assigned may probably suffice to justify

\* Loc. cit. p. 60.

† Die fossile Flora der permischen Formation.

‡ Proceedings of the Lit. and Phil. Soc. Manchester, vol. xi. no. 7, p. 69.

me in following M. RENAULT'S example, assuming the desirableness of abandoning CORDA'S name of *Palmacites* as misleading in this instance, and COTTA'S term *Medullosa* as belonging to the other species of his genus.

Examples of very young or terminal rachides of *Myelopteris* are not uncommon, since Mr. BUTTERWORTH and the late Mr. WHITTAKER have added specimens of such to those which I have collected myself. More matured petioles are much more rare. In addition to two or three which I have met with, I have received one very fine section from Mr. BUTTERWORTH, and Captain J. AITKEN, of Bacup, has placed in my hands an interesting example; but none of these rival in magnitude the examples from Chemnitz and Autun. M. RENAULT has kindly supplied me with a beautiful specimen from the latter locality.

Fig. 1 represents a transverse section of a petiole, for which I am indebted to Mr. BUTTERWORTH. The section is half an inch in diameter in one direction and  $\frac{5}{16}$  in the other. It consists of a mass of parenchyma (*a*), the cells of which vary in diameter from .006 to others of very much smaller dimensions, encased in a cortical investment (*b*), whilst scattered over the section are numerous gum-canals (*c*) and vascular bundles (*d*). The figure represents this section enlarged ten diameters. Though I have no longitudinal section of this individual example, I have such sections of similar ones which must be studied along with it. Fig. 2 represents a longitudinal section of the central part of a similar specimen to fig. 1, but enlarged 20 diameters. From this latter section we find that the cells of the medullary parenchyma (*a*) are arranged in more or less vertical lines, as is usually the case amongst Ferns, though, as seen in the figure, they are subject to much variation in this respect: this vertical arrangement is due to the tendency of the parallel walls of the cells to arrange themselves at right angles to the long axis of the petiole, a condition well shown in fig. 8.

Figs. 3, 4 & 4\* represent three very young, or rather, perhaps, they may be termed terminal portions of the branched rachis. At the first glance these sections appear altogether different from fig. 1; but the differences are but apparent, since an unbroken series of links connects the two conditions, and shows that fig. 1 is but a more developed condition of fig. 3. Fig. 5 is a longitudinal section of a yet smaller rachis of the same kind as figs. 3 & 4, but giving off lateral branches (*h*), which are probably the petioles of leaflets. This figure is enlarged 16 diameters, the original specimen being little more than .06 in diameter.

In the size and arrangement of their parenchymatous cells these several examples vary but little from what I have just described. In the young or smaller branches of the rachis (figs. 3 & 4), the most conspicuous objects are longitudinal canals, which appear in the transverse sections as large circular openings, varying ordinarily in these young specimens from .005 to .007 in diameter. The interior of these canals is frequently occupied by a slender column of pure coal, as in fig. 4, *c'*. The longitudinal section (fig. 2) exhibits these canals as running parallel with the long axis of the rachis, and having a nearly uniform diameter throughout their entire length. I have not been able

to detect any true walls enclosing them. They appear to be intercellular spaces, and to have served as gum-canals. In one longitudinal section only (fig. 6), in which a very small example of one of these canals accompanies a vascular bundle, the whole being magnified 65 diameters, the canal (*c*) appears as if it had originated in a row of enormously enlarged and attenuated fusiform cells which overlap each other at their oblique extremities. Since this is the only example of the kind which I have met with, I will not venture to affirm that all the canals have originated in the same way. In the young twigs these canals have a diameter varying from  $\cdot 016$  to  $\cdot 004$ , being usually much larger than in the more matured petiole (fig. 1), in which they rarely exceed  $\cdot 01$  in diameter. In another very fine example of a matured rachis, for which I am indebted to Captain JOHN AITKEN, of Bacup, they are very much smaller (fig. 7, *c*), their diameter ranging between  $\cdot 004$  and  $\cdot 0025$ . In another somewhat matured rachis, a portion of a transverse section of which is represented in fig. 9, the canals (fig. 9, *c*) are about  $\cdot 007$  to  $\cdot 004$ , approximating to the diameter of those of the young twigs (figs. 3 & 4). It thus appears that these canals vary in their dimensions in different specimens; but I cannot discover any indication that such variations have any specific value.

The vascular bundles may next be examined. These vary both in different specimens and to some extent in different parts of the same specimen. In fig. 1 we can readily discern that these bundles are so arranged as to form a certain pattern or design. There is obviously a peripheral ring of them indicated by the letters *d*, whilst others occupying the more central parts of the section appear less regularly arranged; nevertheless a second irregular circular series may be traced, reminding us of what exists in certain recent ferns to which I shall call attention. This disposition to form a pattern is a feature that does not occur in endogenous plants. Each bundle consists of a cluster of vessels of various sizes, as seen in figs. 11 & 14, which represent two of the bundles of fig. 1. In fig. 11, for instance, the vessels (*d'*) are compressed and somewhat deranged in position, and are in close association with an enlarged gum-canal (*c'*), the entire cluster, including the canal, being invested by an imperfect sheath (*e*) formed of small cells. In fig. 11 we have one (*d*) of the smaller peripheral clusters, containing but three or four vessels (*d*).

*The Vessels.*—Fig. 7 represents a fine cluster of these as seen in a transverse section made from Captain AITKEN's specimen. In this example the larger vessels (*d*) compress each other so slightly that they retain much of their cylindrical form, the intervals between them being occupied by small cells. The largest of these vessels has a diameter of about  $\cdot 01$ , and the smallest of about  $\cdot 0012$ . The larger vessels are always aggregated on one side of the bundle, and the smaller ones (*d'*) are clustered together much more compactly on its opposite side. Fig. 9, *d* represents part of a section with two bundles from another specimen in which the vessels are much fewer in number, and the very small ones seen at fig. 7, *d'* are almost wholly wanting. In some instances I don't find more than two or three large vessels and one or two small ones. In the young rachides (figs. 3, 4, & 4\*) it is almost impossible to discover these bundles in the transverse

sections, since the vessels thus transversely divided closely resemble the parenchymatous cells, both in size and form; but on turning to such longitudinal sections of similar specimens as are represented in figs. 2-5 & 6, we see that they are abundantly present; but the largest vessels in such specimens do not exceed  $\cdot 0025$  in diameter. The number of vessels in each such bundle is also smaller than in the larger petioles. It is thus evident that the vessels in a bundle increase in number; and as they do so, either some of them increase in size, or those added at the later period expand into larger dimensions than was the case with those first developed. Fig. 4\* is a transverse section of one of the smallest of these petioles that I have yet met with. On comparing its general form with that of the terminal rachides of *Angiopteris erecta* and other ferns, the projecting angles seen at the lower right and left margins of the fossil section, separated from the rounded central ridge by two deep flanking grooves, are seen to correspond exactly with those parts of the recent rachides which actually bear the leaflets. Hence I think I can scarcely be wrong in concluding that fig. 4\* at all events is a section belonging to the terminal leaf-bearing portion of the petiole to which it belonged. It exhibits two very distinct gum-canals at *c, c*; the several larger openings nearer the centre of the section appear to have been similar canals which have become enlarged by some contraction of the surrounding parenchyma, as was probably the case with figs. 3 and 4.

On turning to vertical sections of these petioles, we discover that nearly all the vessels are either of the barred or of the spiral type. The large ones are chiefly of the former class, the spirals being mainly found amongst the smaller ones. Fig. 8 represents a longitudinal section of a bundle from the same specimen as the transverse section (fig. 7). The largest vessels are here seen at *d*, yet smaller ones at *d'*, and others still smaller at *d''*. Fig. 12 represents a single spiral vessel from the same section as fig. 7. The spiral is here formed not by one continuous thread, as in most Exogens, but by at least four parallel ones, as is so common amongst Palms. Carefully prepared sections of vessels like fig. 12 demonstrate that these are not modifications of reticulated tissue, but true spirals, since the threads of lignine seen crossing each other are shown by such sections to belong to the opposite walls of the vessels. In Captain AITKEN's plant I found a very few unmistakably reticulated vessels. I have already mentioned the fact that these vascular bundles are aggregated with varying degrees of compactness. In fig. 7 a considerable quantity of cellular tissue is interposed between the larger vessels; and on turning to fig. 8, *a'* we see two of these sets of intervascular cells, each of which consists of three or four vertical rows of rectangular cells having a diameter of from  $\cdot 002$  to  $\cdot 0006$ . Occasionally these cells are almost cubical, but they are usually elongated in the direction parallel with the vessels between which they are interposed. At figs. 8, *e* & 10, *e* we find a similar series of cells constituting an imperfect sheath to the vascular bundle. In the transverse section this sheath is often either absent or at least imperfect. In fig. 13 we have portions of two of the large vessels (*d*) of a vascular bundle from Captain AITKEN's specimen with part of its investing sheath at *e, e*. The cells of the latter graduate rapidly into the ordinary interfascicular parenchyma.

The same appearance is observable in fig. 14, where, at *e*, we find a similar sheath. This latter bundle belongs to the specimen fig. 1. In some few instances I find a few prosenchymatous fibres entering into the composition of the sheath; but this is far from being a constant feature.

I have already described the numerous isolated gum-canals which enter into the structure of these petioles; but besides these we have numerous others associated with the vascular bundles. In the section (fig. 1) it will be seen that every one of the vascular bundles has connected with it a large round or semilunar orifice. In the enlarged fig. 14 one of these orifices (*d'*) is clearly seen to be enclosed within the cellular bundle sheath *e*. At first I was convinced that each of these was a large gum-canal which formed part of the bundle. Fig. 9 represents a small portion of one of several sections which I made of one specimen, in which very few bundles exhibit any trace of similar canals closely associated with the bundles, though such canals exist independently (fig. 9, *c*) in large numbers and of conspicuous size. On dissecting Captain AITKEN's specimen, I found that many of its bundles were as devoid of open spaces as fig. 9. Others had semilunar lacunæ like those of fig. 1, whilst others were so exceedingly large and irregular as to form a cavity entirely surrounding the vascular bundle. One of these irregular orifices is seen in fig. 7, *d'*, *d'*; and on comparing it with the small gum-canals (*c*, *c*) in the same figure it becomes obvious that they are different structures. These and other similar facts led me to distrust my first conclusions, and made it probable that these open passages were rather spaces caused by the detachment of the vascular bundles from the surrounding cellular tissue, such as we frequently observe in sections of the recent Lycopods. Further studies of these sections led me to conclude that the explanation may be found in a combination of these hypotheses. Thus in fig. 8, *c* we have an unmistakable gum-canal associated with the large bundle represented there. In fig. 5, *c* similar combinations exist. In fig. 10, on the other hand, which is a longitudinal section of one of the bundles belonging to the same specimen as fig. 8, we have no gum-canal. Yet, as I have already shown, we cannot for a moment believe fig. 7, *d'* to represent, in any sense, the small canals (*c*, *c*) of the same figure. I conclude, therefore, that such canals are wholly absent from some bundles as in fig. 9; that they are distinctly present, but of small size, in such bundles as fig. 8, *c*; that they exist in similar position, but of much larger dimensions, in such cases as figs. 1, 2-6, & 14; and that in examples like fig. 7, such a canal, devoid of any true walls (being, in fact, a mere intercellular space), has constituted a weak point, which has been converted into a larger irregular cavity by the shrinkage of the neighbouring cellular tissues\*.

There yet remains to be considered the cortical layer of this curious plant. Here again we meet with variations in different specimens. In very young rachides, like

\* Since writing the above I have dried thin sections of the recent petioles of *Angiopteris erecta* between two plates of glass, and found that lacunæ were formed contiguous to each vascular bundle exactly corresponding with those seen in my fossils. This observation puts the origin of these large lacunæ in mechanical shrinking of the parenchyma surrounding the vascular bundles beyond the reach of doubt.—June 1st, 1876.

figs. 3 & 4, we find little more in each transverse section than a thin layer of a tissue (*b*) which is much more dense and opaque than the parenchyma which it encloses. Its inner margin is irregular. Longitudinal sections, like fig. 5, indicate that this tissue consists of compact prosenchyma, though in these specimens the mineralized condition is not favourable to the display of the details of its structure. In tangential sections of somewhat larger rachides we see this prosenchyma (*b*) is grouped in longitudinally disposed bands (fig. 15, *b*), which subdivide and again coalesce with each other at irregular intervals. These prosenchymatous cells appear to be slightly thickened by internal deposits, and have a diameter of from  $\cdot 00125$  to  $\cdot 00062$ . In the above section the spaces between the prosenchymatous bands are occupied by prolongations of the medullary parenchyma (*a*). In the specimen, fig. 1, these fibrous bands are arranged in the transverse section as a series of small wedges, the contiguous bases of which form the outer boundary of the section, whilst their narrowed inner angles are separated by corresponding but inverted wedge-shaped prolongations of the medullary parenchyma. This arrangement is clearly shown by fig. 16, which represents a small portion of the cortical layer of fig. 1, further enlarged to 80 diameters. The coalesced bases of the prosenchymatous wedges are seen at *b*, *b*, and the outward prolongations of the medullary parenchyma (*a*) are seen at *a'*, *a'*. Since this section is made from a petiole that was wholly detached from the outer matrix, I cannot be sure that it exhibits the entire peripheral portion of the cortical tissues. But whether it does so or not it will be noticed that the fibrous wedges are arranged with considerable regularity in one linear series, and that no detached prosenchymatous bundles exist within that linear series. On turning to fig. 17, which represents a similar section to the last, but taken from Captain AITKEN's specimen, we see that we not only have, at *b*, the wedges similar to those in fig. 16, but in addition we have an inner series of detached rounded or elliptical bundles at *b'*, *b'*, and a further set of crescentic ones at *b''*, *b''*, the latter being in contact with the large gum-canals (*c*, *c'*) which abound in the cortical portion of the section. In the section (fig. 16) the cortical layer has a thickness, measuring from the base to the apex of each wedge, of about  $\cdot 016$ . The area occupied by the prosenchymatous bundles in fig. 17, amounting to  $\cdot 03$ , including the detached ones, will sometimes be rather greater than in fig. 16. In the specimens described thus far I find no definite trace of any layer external to the prosenchymatous one; but I have some examples in which I find clear evidence that in them the parenchymatous tissues are prolonged beyond the prosenchymatous ones, and appear to constitute a yet more peripheral layer of parenchyma. This is very clearly shown in sections made from the same specimen as that of which fig. 17 represents a portion. When this is the case the whole of the prosenchymatous bundles become enclosed in parenchyma, and converted into more or less completely detached hypodermic islets. This condition is somewhat important to us when we endeavour to ascertain the homologies of these structures in relation to living Ferns.

Similar prosenchymatous bundles to those just described, but of smaller size, occur

in some of my specimens in the more central parts of the rachis. I have already mentioned that a few fibres occasionally unite with the small parenchymatous cells to compose the imperfect sheath of the vascular bundles. But besides these we find free bundles, occasionally in contact with a gum-canal. At other times I discover one or two such outside, but not far removed from the sheaths of the vascular bundles. Fig. 13 represents one of these bundles enlarged 350 diameters; *d, d* are portions of two of the vessels belonging to a large vascular bundle, of which, as we have already seen, *e, e* is the cellular sheath and *g* is the prosenchymatous bundle composed of thickened fibres and imbedded in the medullary parenchyma. In the specimen figured a second bundle existed in similar relationship to the vascular bundle *d d*.

There yet remains to be considered the branching of these petioles. In fig. 5, which in all probability represents one of the ultimate subdivisions of the true rachis, we have a distinct branchlet given off at *h*. From its size I imagine this must have been the small petiole of a leaflet; a second and similar one is obviously being given off at *h'*. If these are, as I suppose, the ultimate petioles of leaflets, the latter have been arranged in this specimen, at least, at intervals of about half an inch apart. In another of my examples a rachis of about a quarter of an inch in diameter is giving off a lateral branch of about an eighth of an inch in diameter. In both these cases the secondary branches are given off at right angles to the primary one, and not obliquely, corresponding in this respect to their arrangement in the *Myelopteris Landriotti* of M. RENAULT\*.

In fig. 1 a large cylinder of cellular tissue, with a vascular bundle within it but pushed out of its normal central position, is seen at *x*. This is a small rootlet of *Stigmaria* which, as is so often the case, has forced its way into the ruptured interior of the petiole.

These descriptions will, I think, make it plain to the experienced student of vegetable organography that the subject of them cannot be a Palmaceous Monocotyledonous plant. The structure of the vascular bundle, especially the restriction of its vascular tissue to spiral and barred forms, with the absence of all traces of phloem-structures, makes this sufficiently obvious. In like manner, though at first sight its remarkable layer of hypodermal woody prosenchyma bears a superficial glance to the peripheral fibre-bundles of a palm, yet their structure and arrangement are very different in the two cases. It was the peculiarities displayed by these two tissues that led me to seek for the true affinities of those plants amongst the Marattiaceæ, their close resemblance to which, as I have already mentioned, I demonstrated at the Meeting of the British Association for the Advancement of Science in September 1873. My friend Professor RENAULT announced that he had arrived at the same conclusion, after studying the Autun examples of this type, in his memoir presented to the Academy of Sciences at Paris in January 1874. At that time we had not exchanged our views on the subject; hence our united, but independent, testimonies render our joint conclusion an exceedingly probable one. I may observe that there is no doubt that the Autun plants corre-

\* Comptes Rendus, 26 Janvier 1874.

spond very closely with mine from the Oldham Upper foot-coal and Ganister-bed. The principal difference between the French and English examples that I have seen is in their size, some of the former being nearly four times the diameter of the largest of those which I have obtained from our older coal-fields. I am indebted to M. RENAULT for a beautiful specimen from Autun which is fully two inches in diameter. I have, as yet, met with nothing like this in our Lancashire beds; but it corresponds closely enough with the dimensions of the swollen bases of the petioles of *Angiopteris erecta* and others of the larger Marattiaceæ. M. RENAULT finds the gum-canals in his specimens more numerous in the centre of the petiole than at its circumference. In mine these canals are pretty equally distributed over the entire transverse section. Such canals are found abundantly in most of, if not all, the Marattiaceæ, though they are not confined to this aberrant type of the Ferns. I find them very well represented in the petioles of *Cibotum princeps*.

In the petioles of *Marattia fraxinea* and *M. laxa* these canals are of large size, but chiefly found in the medullary parenchyma, especially in its more central portions, being wholly absent from the hypodermal prosenchyma.

On the other hand, in *Angiopteris Teismaniana*, *A. erecta*, and *Marattia ascensionis*, they not only exist in the parenchymatous portions, but they are equally abundant, though of smaller size, in the dense layer of sclerenchyma\* which encases the inner parenchyma. In several of my figures of the fossil forms I have represented these canals as being more or less filled with a cylindrical rod of black carbon, as in the example of fig. 17, *c'*. I have seen nothing like this in any of the vascular tubes, whilst in the canals it is the common condition. It appears to me that this difference is due to something more than mere infiltration of carbonaceous matter in the case of the inter-cellular canals; in all probability the black substance is the carbonized residuum of the gum with which these canals were once filled.

M. RENAULT has already called attention (*loc. cit.*) to the fact that whilst in our fossil examples the hypodermal sclerenchyma forms an interrupted layer, in the recent Marattiaceæ it forms a continuous one. The inner margin of my sections of *Angiopteris erecta* display an irregular dentate outline, which approaches in some slight degree to that of fig. 1. M. RENAULT has further pointed out that ordinarily in *Angiopteris* there are isolated bundles of sclerenchyma within and detached from the continuous hypodermic layer. As already shown, I find these islets to be wanting in *Marattia laxa* and *M. fraxinea* (that is, in the two species which exhibit no gum-canals in the sclerodermic layer), whilst they are present in *Angiopteris Teismaniana*, *A. erecta*, and *Marattia ascensionis*; they are also more conspicuous in the thick bases of the petioles than in their slender upper extremities.

The differences in the thickness of the sclerenchymatous layer in my specimens

\* I have used this word, not in the limited sense in which it is employed by METTENIUS, but in the broader one suggested by SACHS in his 'Lehrbuch der Botanik,' 2nd edition, p. 76, where he proposes the application of the term to all hardened prosenchymatous as well as parenchymatous cells.

figured is probably due to age, since I find that in *Angiopteris erecta* this layer is scarcely visible in the ultimate leaflet-petioles, but is from  $\cdot004$  to  $\cdot008$  in the secondary rachis. In the upper portions of the primary rachis, where the latter has a diameter of about three eighths of an inch, this layer has a thickness of about  $\cdot016$ , whilst near the base of the same petiole, where the latter has a diameter of nearly 2 inches, the sclerenchyma is nearly  $\cdot05$  in thickness. Similar conditions appear to have prevailed in our fossil forms.

In all the recent examples of Marattiaceous Ferns we have a very distinct ring of parenchyma external to the sclerenchymatous cylinder; which parenchyma is often more or less completely separated into three layers by the development in its more central cells of a quantity of chlorophyl. This superficial parenchyma is very distinct in all the species which I have examined, but is the least developed in *Marattia fraxinea*. I have called attention to the existence of indications of a similar layer external to the sclerenchyma of some of my fossil examples; but these specimens have not enabled me to detect the epidermal layer, with its stomata-like openings, which Professor RENAULT has found in his well-preserved silicified fragments.

Whether or not all my fossil examples belong to the same species may be doubtful, since they exhibit considerable differences in the diameters of their gum-canals; but as many of these may, as in fig. 4\*, have undergone some alteration in size owing to contraction of the parenchymatous cells, I think it unsafe, in the present state of our knowledge, to make these differences specific features. There are also differences in the structure of the sclerenchymatous hypoderm, as shown in figs. 16 & 17; but I cannot satisfy myself that these differences have more value than the variations in the canals.

The specimens next to be described also belong to the class of Ferns, and are interesting because they show that the fossils with which we have so long been familiar from the coal-fields of the continent under the general name of *Psaronites* are not absent from the Lower Coal-measures of Lancashire; but though the evidence I am about to advance clearly shows the correctness of the above statement, it must be confessed that our representatives of this group of objects present themselves in very humble guise contrasted with the magnificent examples of *Psaronius* and *Protopteris* figured in the pages of CORDA's 'Flora der Vorwelt.'

The probable existence of tree ferns in the British Coal-measures was long ago pointed out by the late Professor Phillips, and by the authors of the 'Fossil Flora of Great Britain.' But these observers derived their conclusions solely from the external forms of certain stems. At the Meeting of the British Association for the Advancement of Science in 1872, Mr. CARRUTHERS described what he believes to be eight forms additional to the two figured in the 'Fossil Flora' of LINDLEY and HUTTON. All these examples appear to have been obtained from the Bath coal-field. Hence I believe that the specimens of this group which I am about to describe are the first that have been

met with in the coal-fields of Lancashire\*. Some of them I have obtained myself. For others I am indebted to Mr. BUTTERWORTH; but for my best examples I had to thank the late Mr. J. WHITTAKER†.

With two exceptions my specimens are confined to small masses of the adventitious roots so characteristic of the *Psaronites* and arborescent Ferns; but in two instances I have obtained the outer layer of epidermal and subepidermal tissue from which the rootlets more immediately sprang. Fig. 18 represents a transverse section of one of these of the natural size; the outer or cortical parenchyma of another specimen with several rootlets passing downwards and outwards through it is enlarged 24 diameters in fig. 19. This cortical layer consists of a somewhat irregular parenchyma, composed of cells which are usually from about  $\cdot 01$  to  $\cdot 006$  in diameter. At the innermost portion of this cortex (fig. 19, *b*) the structure is somewhat confused; the regular parenchyma has interspersed through it a number of irregular cavities, each of which seems to have been either a large cell, or to have resulted from the rupture of two or three cells which have united to form a common cavity. As we proceed outwards, the cells (*b'*) become somewhat larger than at the inner portion of the cortex. At *i, i* we have several rootlets seen in transverse section, some of them being divided into two halves by an accidental fissure which has extended through this portion of the bark and been filled up with infiltrated crystalline carbonate of lime. At *b''* we find the parenchymatous cortical cells increasing still further in size, becoming lax in their aggregation, and finally being prolonged into a number of epidermal hairs such as frequently clothe the adventitious roots of living tree ferns—such, for example, as *Cyathea dealbata*.

Fig. 20 represents an enlarged portion of fig. 18, which latter is a cluster of adventitious rootlets free from the cortical parenchyma which encloses them in the case of fig. 19. Here the interspaces between the rootlets are seen to be occupied by numerous epidermal hairs. Fig. 21 is a portion of fig. 19 yet more highly magnified.

Each rootlet, when free from the cortical parenchyma, has a diameter of from  $\cdot 075$  to  $\cdot 12$ . Externally it consists of a very well-defined cylinder of sclerenchymatous prosenchyma (figs. 20 & 21, *l*). This cylinder-wall is from  $\cdot 012$  to  $\cdot 015$  in thickness. The fibres of which it is composed have a diameter of from  $\cdot 00125$  to  $\cdot 003$ . Within this cylinder there has doubtless been a mass of cellular tissue, which has disappeared in every instance that I have yet seen; but each rootlet retains more or less distinct traces of the central bundle of small vessels (fig. 20, *m*). Their state of mineralization prevents my determining their characters with absolute certainty; but some of the fragments indicate that

\* Since this Memoir was read I find that fragments of tree ferns with aerial roots were figured and described by the Rev. HENRY H. HIGGINS, M.A., "On some Fossil Ferns in the Ravenhead Collection, Free Public Museum, Liverpool," p. 3, pl. 11. figs. 2 & 3,—June 2nd, 1876.

† I much regret that since my last memoir was read I have to speak of this valuable auxiliary in the past tense. He was an excellent example of the scientific operative for which Lancashire has so long been celebrated. His zeal for the investigation of the plants of the Coal-measures was only equalled by the open-handed liberality with which he placed his valued treasures at the disposal of any one who was able and willing to use them for scientific purposes.

they belong, as might be expected, to the barred type. They are very distinctly preserved in a transverse section of one rootlet, in which the bundle consists of about a dozen vessels, of which the largest have a diameter of  $\cdot0025$ , whilst the smallest are not more than  $\cdot0008$ . This bundle is represented in fig. 22. The epidermal hairs (figs. 20 & 21, *k*) are extremely numerous and well defined; they are cylindrical, and composed of a single linear series of cells with rectangular transverse septa, which are often indistinctly seen. Their diameter averages  $\cdot0017$ . The length of the cells is variable, but those which I have measured are usually about  $\cdot015$ . Fig. 19, *b''* shows that these hairs are but extensions of the outermost interradicular parenchyma (*b'*).

In the absence of all trace of the more central and vascular portions of the main axis to which these adventitious rootlets have belonged, it is impossible to determine to what class of Ferns they belong\*. In the form of the vascular bundle of the rootlet it

\* As stated above, when my memoir was written I had found no trace of the vascular axis of the plant here described; but the day before this memoir was laid before the Royal Society Mr. CARRUTHERS kindly showed me some sections of the plant from his cabinet, amongst which was one of which fig. 22\* is a representation, of the size of nature. In the upper left-hand corner of this section there is preserved a small portion of a central stem. This part of the section is further enlarged ten diameters in fig. 22\*\*, in which *dd* is a narrow lamina of vessels which appears in the transverse section as a semicircular band. These vessels are not arranged in any regular radiating order, and exhibit no trace whatever of having received any increase to their number from exogenous growths. The character of the vessels does not appear in the transverse section, and unfortunately no longitudinal one appears to have been made of the specimen. The vessels vary in size; but the greater number of them have a mean diameter of from  $\cdot0033$  to  $\cdot005$ , some few being larger and others smaller than these dimensions. This vascular belt is interrupted in the middle; but whether this break is an accidental rupture, or whether the two halves represent parts of separate crescentic masses, is not certain. This vascular lamina has evidently been imbedded in a mass of very regular parenchyma, an inner portion appearing at *a*, whilst fragmentary portions remain of a peripheral mass which has occupied the interval between the vascular layer and the periphery of the stem from which the numerous rootlets (*i*) have sprung. The inner parenchyma (*a*) and the inner portion of the outer parenchyma correspond very closely, and consist chiefly of cells that have a diameter of from  $\cdot0025$  to  $\cdot005$ . But the more peripheral portion of the outer tissue consists of a dense mass of very regular, small, thick-walled cells, with a diameter of from  $\cdot001$  to  $\cdot0006$ , approximating closely in their appearance in the transverse section to the fibres constituting the outer layer of each rootlet. A curious feature of these parenchymatous structures is the presence in them of numerous longitudinal canals (*c, c*), which appear to be identical with the gum-canals of the *Myelopteris* described in the earlier part of this memoir.

Whether the stem originally contained a single circle of these vascular laminae, or whether there were successive layers concentrically arranged, as in many species of *Psaronius* figured by CORDA, is not determinable from Mr. CARRUTHERS's sections. The great probability, however, is that the latter condition has existed. It will be observed that this, the only stem of a tree fern from the British Carboniferous deposits of which the internal organization has hitherto been described, exhibits the same absence of all exogenous growths as that to which I called attention in some of my previous memoirs as characterizing the continental *Psaronites*. So far as my present experience has extended, all the fossil ferns had, like their recent allies, closed vascular bundles; whilst the Calamites and Lycopods, including in the latter group the *Asterophyllites*, had open ones. If *Lyginodendron* and *Heterangium* ultimately prove to be stems or rhizomes of Ferns, of course this generalization will have to be discarded; but I have as yet obtained no such proof.

Mr. CARRUTHERS's cabinet contains a beautiful section of *Myelopteris*, in which the outer vessels of each vascular bundle are small, but with unusually thick walls, as seen at *d'* in fig. 7\*, which represents one of these bundles, with a small portion of the surrounding parenchyma, much enlarged.

approaches nearest to CORDA'S *Psaronius radiatus*; but it differs wholly from that plant in the cellular hairs with which its roots are clothed. The only plant which CORDA has described in which the roots are similarly furnished is his *Protopteris Cottai*; but in that plant the sclerenchymatous cylinder of each root is invested by a thick composite layer of parenchymatous cells, whereas in my plant the hairs spring abruptly from the exterior of the sclerenchymatous cylinder. As this appears to be an undescribed species, I may be permitted to dedicate it to my friend Professor RENAULT, from whose labours amongst the fossil plants of Autun so much good has already arisen, and is likely yet further to arise. Our investigations, proceeding side by side, mutually illustrate each other, and will eventually afford the means of establishing some trustworthy comparisons of the flora of the French coal-field with that of Lancashire. I propose to designate my plant the *Psaronius Renaultii*. It is of course possible that it may some day be proved to be the base of a *Caulopteris*, or some other of the supposed tree ferns whose stems have already been discovered in the Coal-measures.

The next plant which I propose to describe is one of the most remarkable as well as the most beautiful of those which I have met with in our Lancashire deposits. On the first glance at its structure we might suppose the Carboniferous forests to have been hung with Bignoniaceous Lianas like those of Brazil; but closer examination demonstrates that this resemblance is only a superficial one. At the same time a remarkable instance is furnished by this plant of those resemblances between very different objects that have of late years attracted the attention of botanists. Figs. 23-26, 32, 33, 34, 37, and 38 show the vascular portions of the stem arranged usually in six, but, in the case of the two last-named figures, respectively in five and four wedges, separated by corresponding inward prolongations of the cortical tissues—a condition which forcibly reminds the botanist of similar transverse sections of the stems of Bignoniaceæ. But further examination shows that my fossils are very different from that recent type, since their central axis is, like that of some of the arborescent Lycopodiaceæ which I have already described, composed of a mass of vessels. This axis forms the nave-like centre from which the six large vascular wedges radiate like the spokes of a wheel, each of these primary wedges being separated by medullary rays into a multitude of secondary ones. The bark is differentiated into several distinct portions, and the whole structure is invested by the double row of vertically elongated cells indicated by the letter *k* in each of the figs. 23, 24, 25, 28, & 36. That the six radiating primary wedges are the products of exogenous growth is clearly shown by the sections of young twigs represented by figs. 24 & 25, in which specimens the central vascular axes alone exist—a condition of things reminding us strongly of what I have already described in the stems and twigs of *Asterophyllites*, and of some of the Lepidodendroid plants. I think there can be no doubt but that, as in the case of the triangular axial bundle of *Asterophyllites*, each of the hexagonal ones of figs. 24 & 25 represents the axial bundle of a young twig, and that the radiating vascular laminae constituting the six primary wedges are the results of exogenous processes of growth, which have converted leafy twigs or branches into matured stems.

Each of the numerous specimens figured in this part of my memoir exhibits some morphological feature, important to be noted, in a better state of preservation than in the other examples. Hence, instead of describing each specimen separately, it will be convenient to examine successively the several structures constituting the plant, proceeding from within outwards. Since it appears easy to identify the homologies of this plant with those of *Lepidodendron* and *Asterophyllites*, I shall revert to the letters of reference employed in the memoirs describing those plants, to represent what appears to me to be identical or closely related structures in each of these three types of organization.

The central axis (*c*) in fig. 23 has a diameter of  $\cdot 04$ . In figs. 32, 33, & 34 its diameter is  $\cdot 024$ , the central tissues in these three sections having been destroyed. In fig. 26, which is a section from the same stem as the last three, but about half an inch higher up than fig. 34, it is rather larger; but it has been subjected to a little lateral compression, giving it an oval instead of a rounded outline. In fig. 25 it is  $\cdot 028$ , and in fig. 24 it is  $\cdot 024$ . In fig. 37 it is  $\cdot 008$ , whilst in fig. 38 it only consists of a few vessels. The entire diameter of the stem in fig. 23 is about  $0\cdot 1$ , whilst in figs. 32–34, had the bark been perfect, it would probably have been about  $0\cdot 14$ .

So far as I can ascertain, this central axis consists wholly of a bundle of vessels, which vary in size. The more conspicuous, larger ones in fig. 23 vary from  $\cdot 005$  to  $\cdot 0025$ ; in fig. 37 the largest are not more than  $\cdot 0012$ , whilst in the young twig (fig. 25) the largest of them average about  $\cdot 0025$ . It thus appears that they increase in size with the age of the stem, judging of that age from the degree of development of the exogenous cylinder. I have not succeeded in obtaining proof of the existence of any cellular tissue mingled with these vessels; neither do they display any regularity in their arrangement; irregular clusters of the larger vessels are connected by smaller ones, as represented in figs. 23 & 26. Those occupying the periphery of the bundle are generally uniformly smaller than is the case with those of the more central portion. In the two young twigs (figs. 24, *c* & 25, *c*) the entire bundle has a distinct hexagonal transverse section; but this definite hexagonal contour is scarcely traceable in those examples which possess an exogenous zone. Longitudinal sections show that all the vessels of the central axis are, like those of the exogenous wedges, of the reticulated type (fig. 29, *e*). I have not yet discovered in any of my sections a single barred or spiral vessel.

*The Exogenous Zone.*—As already stated, this consists of from four to six separate primary wedge-shaped masses of vessels, each of which is composed of numerous laminae in which the vessels are arranged in regular radiating series. In every one of what appear to be adult stems, such as figs. 23, 26, 32, 33, & 34 these wedges are six in number. The innermost vessels of each wedge are somewhat smaller than the more peripheral ones. In fig. 1 the largest peripheral vessels are about  $\cdot 0025$ ; in fig. 32 they are about  $\cdot 0037$ ; in fig. 37 the larger vessels are also about  $\cdot 0025$ . The number of the radiating lines of vessels seen in a transverse section of each primary wedge varies even in the same plant. Still more so when we compare figs. 37 & 38 with those of the more matured stems. The number of vessels composing each radiating

series obviously varies with the age of the axis. Even in the transverse sections the existence of medullary rays is sufficiently obvious. In fig. 31, which represents a small portion of the periphery of one of the primary wedges of fig. 34, these medullary rays are clearly shown at *f*, where they appear as parenchymatous cells elongated radially. Fig. 30 is a tangential section of a stem intersecting three vascular wedges, the central one (*d*) having been cut through at its innermost portion close to the central vascular axis. In this section the medullary rays appear at *ff*, as clusters of cells arranged vertically as single linear series. In fig. 27 we have a tangential section of a similar wedge at its more peripheral extremity. These two sections combined illustrate the increase in diameter of the vessels composing each primary wedge as we proceed from within outwards; and fig. 27 further demonstrates a corresponding increase in the number and dimensions of the medullary rays (*f*). In the latter figure we find that many of these rays are lengthened vertically by a material increase in the number of their component cells; and, further, that from time to time we meet with portions of these rays, as at fig. 27, *f'*, in which two and even three vertical lines of cells coexist in the same ray. Fig. 29 represents a portion of a slightly oblique, radial, longitudinal section crossing two vascular laminae (*e*, *e'*), with parts of the medullary ray (*f*) which separate them. The latter exhibits the usual mural arrangement of its cells seen in radial sections of so many others of the Carboniferous plants. In the tangential section (fig. 27) the vertical length of these cells ranges from .001 to .0025.

*The Cortex.*—This part of the organism exhibits some very characteristic features which distinguish the plant under consideration from any of those which I have hitherto described. The six large primary wedges of the vascular zone are separated by a mass of delicate thin-walled parenchyma. The arrangement of the cells of this structure is best shown in the two figures 26, *h* & 32, *h*. The cells are parenchymatous, but are elongated radially, showing a tendency to arrange themselves in lines more or less parallel with the sides of the two contiguous primary vascular wedges. On approaching the broad outer extremities of these wedges, the elongated cells exhibit a strong tendency to diverge in two groups, each one bending round the peripheral extremity of the woody wedge nearest to it, whilst in the angular space between and external to the diverging portions we have ordinary regular parenchyma. I do not mean to convey the impression that all these portions of the cellular tissue are separated by clearly defined boundaries; such is not the case; but whilst these respective areas graduate into each other, there is little difficulty in tracing broadly their respective characteristic features, which are well shown in fig. 34, *i''*. The same figure further shows, at *g*, *g*, another remarkable feature; the cellular masses (*h*) do not bend round the outer extremities of the primary wedges (*d*, *d*) as just described, in immediate contact with those wedges; but they enclose a small semilunar area (*g*) coextensive with the diameter of the wedge, and which is occupied by a distinct form of cellular tissue. I shall shortly give my reasons for believing that this latter tissue is a quasi-cambial meristem layer, which is concerned in the formation of the newest exogenous vascular growths. The general features of

the cells of this meristem tissue are shown in fig. 31, *g*. The outer extremities of all the medullary rays terminate in it; and as they do so those of opposite sides of each primary wedge bend inwards more or less obviously towards an imaginary line prolonged through the centre of the wedge into the bark. Indications of this arrangement are seen at *g'* in fig. 32.

The usual aspect of the masses of cortical parenchyma separating the primary vascular wedges, as they appear in vertical tangential sections, is shown in several of the figures, but especially in figs. 27, 30, & 35, *h*. In these sections it appears as ordinary parenchyma, whilst in radial sections of the same tissue its cells exhibit a tendency to arrange themselves in semimural fashion, as seen at fig. 27, *h'*.

External to the cortical structures just described is another and yet more extensive one, which appears to have been the primitive tissue of these stems. I infer this from the fact that in the young twigs (figs. 24 & 25) it is the only cortical tissue observable, except the epidermal layer (*k*), and occupies the entire area between that layer and the central vascular bundle (*c*). Its thickness relative to the size of the stem is also well seen in fig. 23. It consists of a coarse but thin-walled parenchyma, the cells of which are of unequal sizes, but generally about  $\cdot 005$ . The mean thickness of this layer in fig. 23 is about  $\cdot 025$ . It appears distinctly in figs. 32, 33, & 34, *i*, investing both the vascular axis of the primary stem and the branch which is being given off from the latter; whilst in fig. 34, in which the vascular area of the branch is entirely separated from that of the main axis, it constitutes the chief portion of the separating layer. In the three sections just referred to, whilst we see the tissue in question enclosing the more internal layers of the bark and their associated vascular areas, it will also be noticed that in passing over the cellular radii which separate the six large vascular wedges it dips inwards towards the centre of the stem. This arrangement is well seen in fig. 34, *i'*, *i''*.

Another of the characteristic features of this very remarkable plant is found in the distinct epidermal layer (*k*) with which it is shown to be invested in figs. 23, 24, & 25. A more highly magnified representation of the same tissue, as seen in the transverse sections, but enlarged 284 diameters, is seen in fig. 28. Viewed in this aspect it consists of two somewhat irregular rows of cells, which are very distinctly different from those of the bark (*i*) which they immediately invest. Those of the outer bark (*i*) have their walls of a dark colour and mottled aspect—a condition apparently due to the carbonization of the cell-contents which characterized them when living. Those of the epidermis, on the other hand, are more clear and transparent, as if they had been originally devoid of all coloured protoplasm or other cell-contents. They are also smaller in size, averaging, in transverse sections, about  $\cdot 008$ , and retain their regular form much more perfectly than the larger and softer cells underlying them. The distinction between these two tissues becomes yet more conspicuous when we turn to the longitudinal section, fig. 36. We here see that the epidermal layer (fig. 36, *k*) is separated from the cortical parenchyma by a sharply defined line, whilst its component cells are

elongated. They vary considerably in their vertical length, those delineated in fig. 36, *k* being longer and narrower than they are in some other portions of the section of which the figure represents a small part; but the tissue is always easily distinguished from that which it invests.

*Exogenous growth.*—The difference between the sections figs. 24 & 25, in which we have merely the primary vascular bundle, and fig. 23 and other similar figures, in each of which what is obviously a corresponding bundle (*c*) is surrounded by six diverging wedges composed of radiating laminae of vessels separated by medullary rays, affords sufficient proof of the existence of exogenous growth in these plants. These wedges exhibit the same evidences of being the result of successive peripheral additions that we have already found in the instances of many other Carboniferous plants. This is especially the case with some, of part of one of which fig. 31 is a representation, enlarged 130 diameters. It is a portion of a transverse section of the same specimen as is represented in the figures 32, 33, & 34. We find at *e, e* the outer extremities of several vascular laminae, separated by the medullary rays (*f, f*), whilst at *g* we have a portion of one of those crescentic masses of peculiar cellular tissue which I have already described as being located at the peripheral extremity (fig. 34, *g*) of each of the six primary vascular wedges. There is no mistaking the evidence that along the line (fig. 31, *e', e'*) a conversion has been going on of the cells of this tissue into true vessels, destined to form outward extensions of the vascular laminae (*e, e*). Oblique longitudinal sections show that the narrow cells (*e''*), which are here being elongated in a direction parallel to the transverse diameters of the vessels with which they are in contact, are also elongated in the vertical direction, and are assuming a vascular aspect. Hence it becomes clear that the cellular tissue *g* is, as I have already stated, a special meristem tissue possessing pseudo-cambial properties, and the active instrument in producing the peripheral vascular growths. It thus appears that in these plants the pseudo-cambial layer never becomes a continuous ring as in most of the other exogenously developed plants which I have already described, but that it remains permanently in the state in which it exists in the first year's growth of a Dicotyledonous Exogen, *i. e.* as a ring of detached masses, in which the interfascicular cambium has never been developed; affording another instance, in the palæozoic vegetable world, in which conditions that are temporary and transitional in ordinary exogens are rendered permanent ones.

It is impossible to study this plant without being reminded of the Bignoniaceous Lianas of the Brazilian forests; but though in these latter plants the woody axis is primarily divided into four distinct radiating wedges, and though these four wedges continue to grow prominently in advance of the spaces occupied by the cortical tissues that separate them, yet even these latter spaces contain a true cambial layer, through the agency of which they become filled up with vascular tissues that gradually encroach peripherally upon the cortical structure; and as they advance, they destroy the perfect form of the Maltese cross which transverse sections of these woody axes exhibit. Hence the resemblance between my fossil and true Bignoniaceous Exogens is more apparent

than real, since in the former the radial inward prolongations of the bark (*h*) never become occupied by vascular structures, whilst, I need scarcely add, the morphology of the cortical layers in the two cases is altogether different.

*Branches.*—In the present state of our knowledge I am unable to ascertain whether figs. 24 & 25 are branches of stems like fig. 23, or correspond to its terminal portions; but be that as it may, I have obtained independent proof that at least one class of branches is given off from similar stems, besides which we have many indications of the existence of another and apparently very different set of secondary lateral vascular bundles. Figures 32, 33, & 34 represent three very instructive transverse sections of one stem, in which the various stages in the development of the branch can be easily traced. These sections were made at intervals of little more than the sixteenth of an inch apart. Fig. 32 is the lowest of the series. The vessels of the central axes have been partly destroyed, and the epidermal layer and some of the subjacent outer cortical layer are also wanting. In other respects the section exhibits in a beautiful manner the more characteristic features of this plant. The two primary vascular wedges (*c*, *c'*) also present much of their usual appearances; but we find that the inward prolongation of the cellular bark (*h'*) separating these two wedges, instead of attaining to its usual dimensions, is narrowed to two or three radial rows of cells (*h*), being encroached upon by a mass of obliquely inclined vessels (*x*), which exhibit every appearance of being given off from the left-hand side of the primary vascular wedge (*c*), and of ascending obliquely from right to left. In the next higher section (fig. 33) the two vascular wedges (*c'*, *c''*) have been pushed widely asunder, and the triangular area between them is now occupied by a number of meandering vessels intermingled with a little cellular tissue. These vessels are proceeding outwards to a semicircular mass of vessels, of which those occupying the centre, whence the others radiate, are arranged without order, like those of the central axis (*c*) of figs. 23 & 26; and the rest are distributed in radiating series, forming numerous exogenous laminae and wedges separated by many medullary rays (*f*). On turning to the third section in the ascending series (fig. 34), we find that the two wedges (*c'*, *c''*) have resumed their normal positions, and that the wedge of cellular bark intervening between them exhibits little or no difference from the corresponding tissue separating the other vascular wedges of the section, save that one or two detached radiating laminae of small vessels pass outwards through its parenchyma. The lateral vascular laminae of the two woody wedges, which are in immediate contact with the intervening bark, have not quite recovered the regularity of radiating arrangement which characterizes them elsewhere. This disturbance of the order is especially seen near the peripheral margin of each wedge. The branch itself now consists of a normal central axis, with its exogenous wedges arranged around that centre, so as to form a complete circular cylinder, which is now entirely separated from the vascular portion of its parent stem by the intervention of a mass of the coarse outer cortical parenchyma (*i*). The radiating series of vessels constituting the exogenous portion of the branch are still seen to be separated by numerous medullary rays of nearly equal size, the separation of these vessels into the six groups seen in

the parent stem not having been perfectly accomplished. Nevertheless there are indications that such a separation is in progress. Thus we see at *h* a mass of cellular tissue separating the vascular masses on either hand of it; not only so, but we discover at the peripheries of three such vascular masses a tendency towards that convergence of the outer extremities of the newly forming vessels of each primary wedge which has been already described and illustrated by fig. 32, *g*. The largest of the vessels in this branch does not exceed .0025 in diameter.

On glancing at fig. 33 the observer is strongly disposed to conclude that the mediating vessels radiating outwards from the parent stem to the half-formed branch were equally derived from the two wedges, *c'*, *c''*; but I believe that, primarily at least, this is not the case. I have already pointed out that in the lowest of the three sections (fig. 32) the aberrant vessels (*x*) unmistakably proceed from the wedge *c*, being separated from *c'* by the radiating extension of the inner bark (*h'*). I have another transverse section of the specimen from which the above three were made, which exhibits a second and similar branch, but which has been so bent in the plane of the section that, though the main stem is intersected transversely, the section cuts through the branch longitudinally. In this case the branch certainly proceeds solely from *one* of the neighbouring primary wedges. In all these sections the vessels of the secondary branches are much smaller than those of the parent stem. It is not impossible that as the branch develops, both the contiguous primary wedges may contribute some vascular elements towards its formation, as appears to be indicated by fig. 33.

In fig. 33 the peculiar cellular tissue which I have termed pseudo-cambial forms an almost continuous semicircular belt around that peripheral upper portion of the branch in which the vascular laminae have assumed their normal radiating order. But in fig. 34, on the other hand, it has begun to concentrate itself into masses at the extremities of the incipient primary vascular wedges, as in the matured stem. This is especially the case at the four points *g, g, g, g*. It is obvious that these several points represent a corresponding number of incipient primary vascular wedges.

Having ascertained these facts, I turned with some interest to the well-known stems of the Bignoniaceæ, to see how far the orientation of their lateral branches corresponded with what I have just described. In these plants there is a distinct medulla, and the lateral twigs are given off in pairs. When this is about to take place, two of the four woody wedges constituting the Maltese cross exhibited by a transverse section of the stem become much broader than the other two, and a prolongation of the pith passes outwards through the centre of each of these enlarged wedges, and carries along with it an investing cylinder chiefly composed of sclerenchyma. Thus each branch springs *from the centre* of a woody wedge, and not from its sides, as in my fossil plant. It follows that in the *Bignoniæ* the areas occupied by the centripetal prolongations of the cortex separating the four arms of the cross take no part in the formation of the branch; whereas we have seen that in my fossil this area is largely concerned in its formation. In one point, however, there is a resemblance between the two cases. In the very

young lateral twig of *Bignonia* the ligneous axis is nearly cylindrical, when it must be invested by a complete ring of cambium ; but this ring clearly becomes broken up, as growth advances, into four detached segments, corresponding to the peripheral extremities of the four large crucially disposed woody wedges seen in more matured stems. Hence in this case the cambial ring, primarily continuous, became an interrupted one. It subsequently again approximated to a continuous one by the development of interfascicular cambium. But whilst on these points there seems to be some analogy between the development of a Bignoniaceous twig and that of my fossil plant, there yet remains an additional distinctive feature. In the former a detached patch of cambium occupies the innermost extremity of each of the four centripetal prolongations of the inner bark which separate the woody wedges, so that these cortical radii are steadily encroached upon by four corresponding radii of wood, which are slowly growing outwards, following, but at a very great distance, the extensions of the four arms of the cross. Nothing like this occurs in my Carboniferous plant. In the latter the six centripetal extensions of the inner bark never become thus converted into a portion of the vascular cylinder.

Figures 37 & 38 represent two transverse sections of the vascular axes of stems of small size. The larger of these has a diameter of  $\cdot 032$ , and the smaller one of  $\cdot 017$ . The larger of these two sections is therefore only about two thirds the size of the corresponding vascular axes of the young branch in fig. 34, the diameter of which is about  $\cdot 047$ , whilst the smaller one is but little more than one third of the diameter of the same branch. The vessels in figs. 37 & 38, like those of the branch referred to, have a maximum diameter of  $\cdot 0025$ . I conclude that these two figures represent the vascular centres of two small branches deprived of their cortical layer. Their chief interest lies in the circumstance that fig. 37 exhibits but five primary vascular wedges, and fig. 38 but four ; whereas every example which I have yet seen, where the stem has attained to what appears to be its normal dimensions, these primary wedges are six in number, as already described. The section of a nodule which contains the two stems (figs. 37 & 38) also contains a third one in their immediate vicinity, and which in all probability belonged to the same plant as the other two : its vascular axis has a diameter of rather more than  $\cdot 1$ . It also has but five wedges ; but one of them is so much broader than the rest as to make it exceedingly probable that it would eventually subdivide into two, and thus complete what appears to be the complementary number of six, characteristic of all matured stems.

The above description makes it obvious that in a very young stage of the development of the exogenous, vascular portion of a stem or branch, the differentiation of the vascular laminae into the six distinct groups, which I have termed primary wedges, is very imperfect, the large radial masses of cellular tissue (*h*) which ultimately separate them being then little more than ordinary medullary rays. If this is true, the mural parenchyma composing them must retain its genetic properties as a meristem tissue, since they certainly become much broader, containing an increased number of cells, as they grow older.

Besides the remarkable branches which I have just described, I find clear evidence of the existence of another, and apparently very different, set of divergent vascular bundles, and which pass outwards through the large cellular radii (*h*) which separate the primary woody wedges. But I find it much more difficult to obtain a clear conception of the nature, origin, and distribution of these bundles than of those previously noticed. In fig. 30 there is represented a condition of which I have seen several examples. In the parenchyma (*h*) separating the two primary vascular wedges *d* and *d'* there is an obvious derangement of the usual condition of the cells of that parenchyma at *y*. The latter display an obvious disposition to be elongated radially, bending outwards to accompany a small bundle of vessels seen at *y*, which is here cut across by the tangential section somewhat obliquely. In fig. 35 we have a similar but more perfectly tangential section of one of the same cellular radii (*h*), with portions of two primary vascular wedges at *d*, *d'*. At *y* we again find a cluster of small vessels passing outwards. At *e*, *e'* we have some meandering vessels detached from direct connexion with each of the two primary bundles (*d*, *d'*), but which obviously contribute to swell the diameter of the intersected bundle, *y*. At *e''* we find a few vessels, separated from those of the primary bundle (*d'*) by a few mural cells of a medullary ray, and which appear to be descending to reach the bundle *y*, towards which their lower extremities bend away from the primary wedge, *d'*. In fig. 36 we again find a similar bundle (*y*) passing through the coarse parenchyma of the outer bark, apparently on its way to escape through the epiderm, *k*. Though I have seen in my sections several other similar indications of these bundles, none of my specimens throw any clear light upon them. That they are distinct from the branches previously described appears very possible; but what is their ultimate purpose I have not yet succeeded in ascertaining. If the vessels *e* and *e''* in fig. 35 really go to the bundle *y*, as they appear to do, there can be no doubt but that they are respectively derived from the two primary vascular wedges, *d* and *d'*. But I cannot yet determine satisfactorily whether the bundle *y* consists wholly of vessels, or of vessels mixed with cells derived from the inner cortical layer through which they emerge. There are indications that some of the cells of the latter are elongated radially to form a sort of sheath to the vessels. All these points are at present but obscurely indicated by my specimens; but the general features of these bundles differ so widely from those of the true branches represented by figs. 32, 33, & 34 as to leave little doubt that they have had a distinct nature, having probably been destined to supply either rootlets or leaves with vessels. Unfortunately my specimens of this very rare plant have hitherto been too few in number to enable me to obtain such a good radial section as might throw light upon these diverticula of the central vascular axis. At the same time it *may* be possible that these bundles pass outwards to become the central bundles of branches corresponding to figs. 24 & 25.

The question of the nature and probable affinities of this plant remains to be examined; and here, again, we have unfortunately to deal with much that is obscure. In the vascular character of its primary central axis (figs. 23-24, *c*) we are reminded of

the vascular axis of the fruit *Calamostachys Binneana* (Phil. Trans. 1874, p. 59 *et seq.*, figs. 33–39), of the stem of *Asterophyllites*, and of the medullary axis of the Lepidodendroid plants described and figured in my second memoir on the Plants of the Coal-measures (*loc. cit.* 1872, Plate 24. figs. 1 & 2). I have already given my reasons for regarding all these three groups of plants as Lycopodiaceous; and it is my conviction that the plant now described belongs to the same natural family. At the same time I need scarcely remark that it differs from all known recent Lycopodiaceæ. Several of the living Lycopods exhibit a defined epidermal layer, investing a cortical parenchyma composed of large cells full of chlorophyl. *Lycopodium alpinum* exhibits this condition; and in *Selaginella Martensii* a similar epiderm, composed of colourless cells, becomes very conspicuous at the margins of the leaflets, where it projects in comparatively large tooth-like, almost unicellular, hairs or spines. But none of these plants exhibit any thing that exactly resembles even the primary central vascular bundle of the fossil form. The nearest approach to it is perhaps to be seen in *Psilotum triquetrum*; but we have nothing resembling the exogenous growth of the six primary vascular wedges in any recent Lycopodiaceous stem. In the peculiar structure of its entire vascular axis this plant stands alone amongst the varied types found in the Carboniferous beds. In the structure of its central vascular axis, especially as seen in the young twigs (figs. 24 & 25), it bears a considerable resemblance to the *Lycopodium Renaultii* described by Professor RENAULT\*; but in the other details of their respective structures I can find few, if any, resemblances between my plant and that of my distinguished friend. In the *L. Renaultii* its discoverer has as yet found no trace of the exogenous growth which is so characteristic of my example.

That the plant is a Cryptogam I think there can be no doubt. It presents no features that indicate a Dicotyledon. All its vessels are mere modifications of the spiral and barred tissue which constitute so universal a feature in the stems of the other Carboniferous Cryptogams. The sclerenchymatous prosenchyma of the woody rings of the Dicotyledons is entirely wanting to its woody zone. It possesses this feature in common with the *Calamites*, *Lepidodendræ*, *Asterophyllites*, and other Carboniferous Cryptogams which I have already described.

In one respect the plant under consideration is one of the most remarkable of any that I have yet seen. Though the largest stem that I have found does not exceed one eighth of an inch in diameter, which is the thickness of that represented in fig. 23, yet its exogenous development is complete. In criticising my views in an early stage of my inquiries, my friend Professor THISLETON DYER expressed his conviction that these supposed exogenous growths were mere questions of size, and had no physiological meaning. But such cannot possibly be the case here. The axis of nearly every known living Lycopod has a diameter equal to that of the fossil before us; yet we find the exogenous structure of the latter as conspicuously developed as in the largest of the Lepidodendroid stems. Whatever

\* “Étude de quelques végétaux silicifiés des environs d'Autun,” Annales des Sciences Naturelles, 5<sup>e</sup> série, Bot., t. xii. (Cahier no. 3), pp. 82–85.

may be the meaning of the prevalence of exogenous development amongst the Cryptogams of the Carboniferous epoch, it clearly has no relation to mere size.

Since the plant now described is remarkably different from any hitherto noticed, I propose to assign to it the generic title of *Kaloxylon*, and to identify it with the name of our distinguished President as *Kaloxylon Hookeri*.

All the specimens which I have figured are from the Oldham Upper foot-coal. But I have found two or three sections of very young branches, in the condition of that represented in the upper part of fig. 34, amongst my sections of specimens from Burnt-island. This circumstance indicates that the genus has had a considerable vertical range, and hence may be expected to occur in some of the continental deposits like those of Autun and St. Etienne, whence I trust that M. RENAULT or M. DE GRAND-EURY will soon succeed in disinterring it.

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 „ fig. 3. Transverse section of a young or of the upper portion of a rachis. Enlarged 20 diameters.  
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*Psaronius Renaultii.*

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*Kaloxylon Hookeri.*

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- „ fig. 38. Similar section to the last, but with four primary wedges. Enlarged 80 diameters.

Fig. 4\*

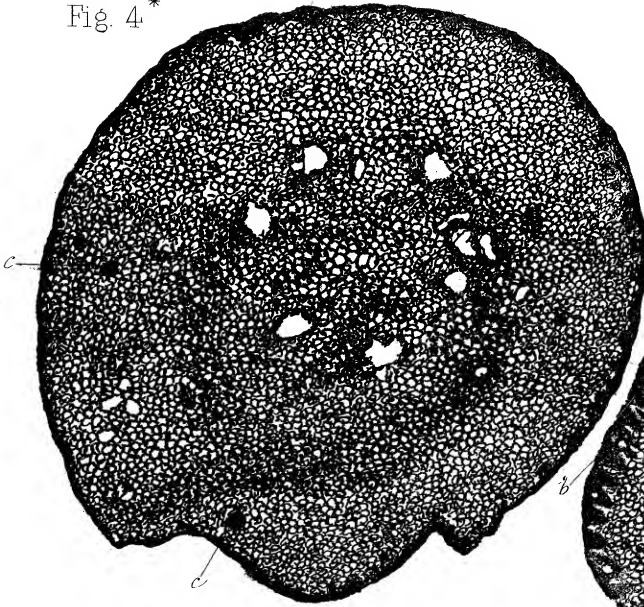


Fig. 1.

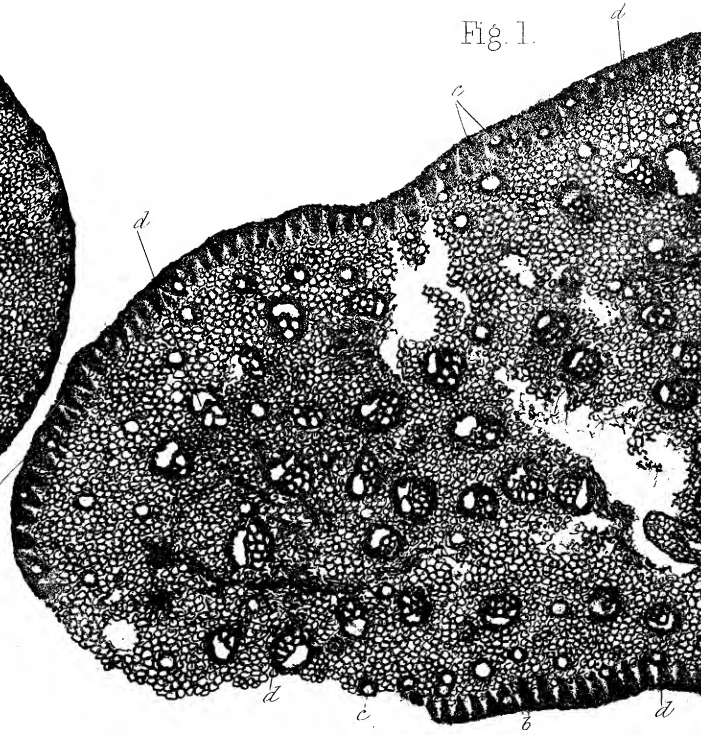


Fig. 2.

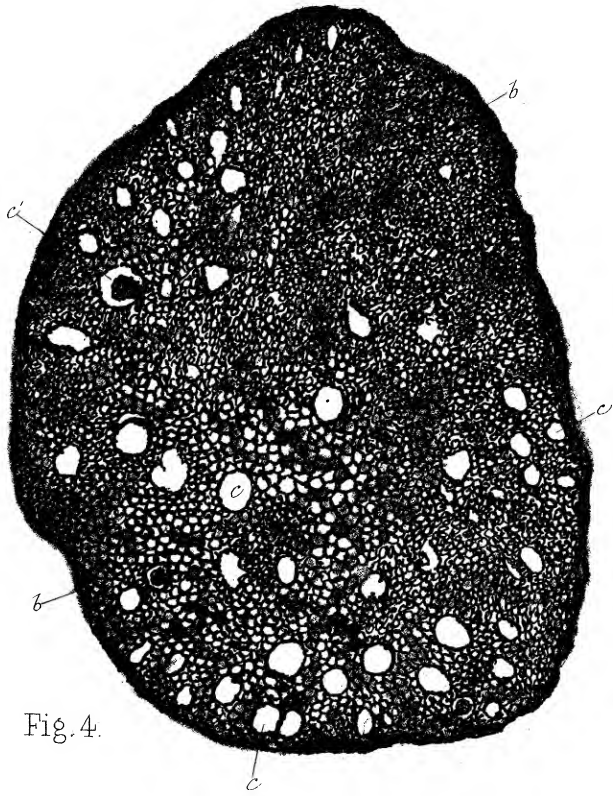
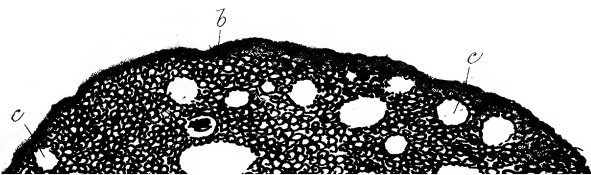
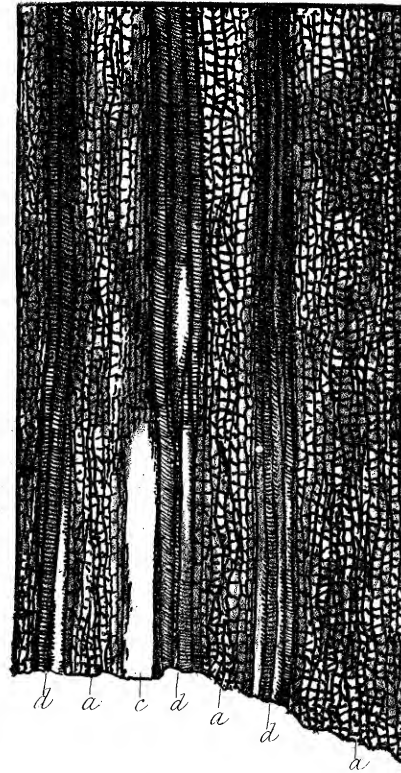
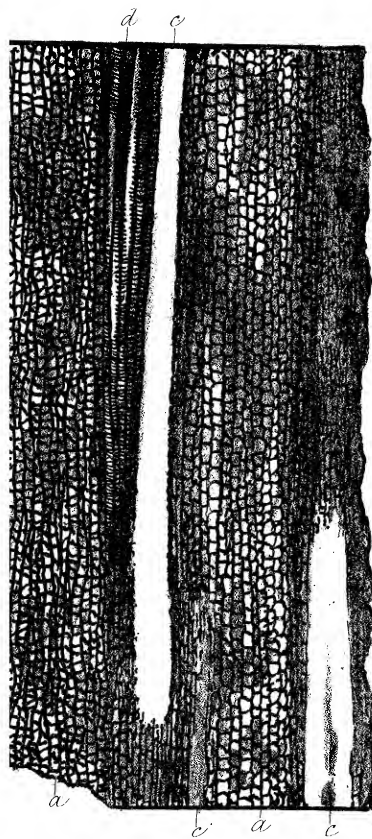
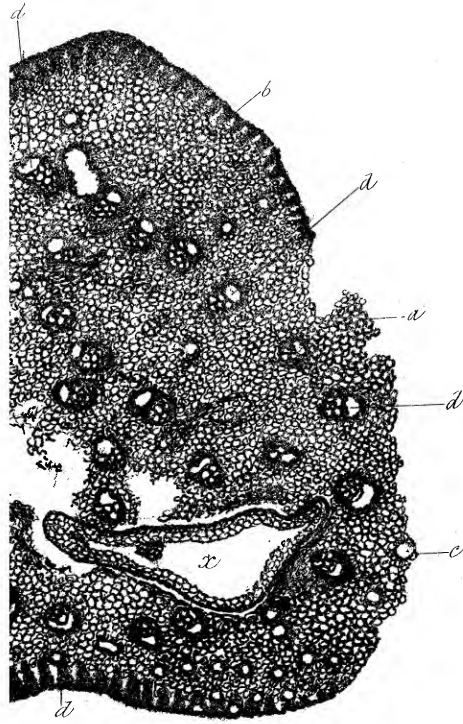


Fig. 4.



Fig 12.





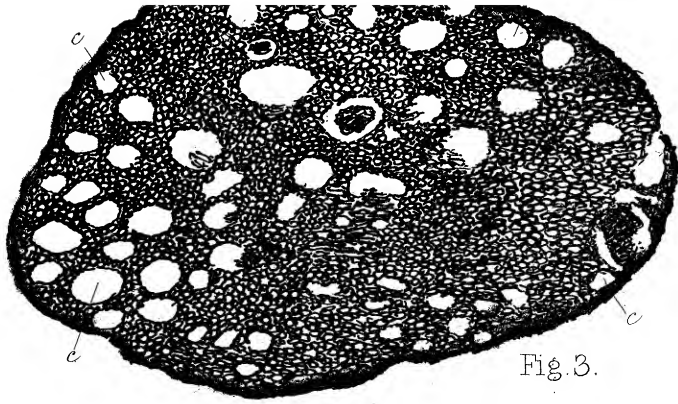


Fig. 3.

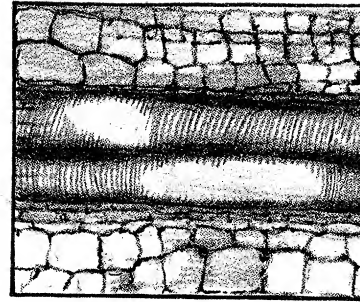


Fig. 10

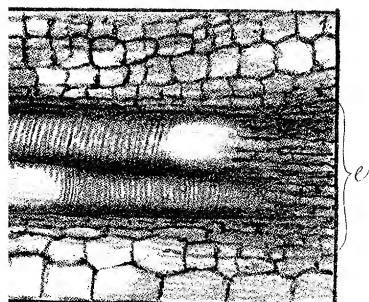


Fig.10.

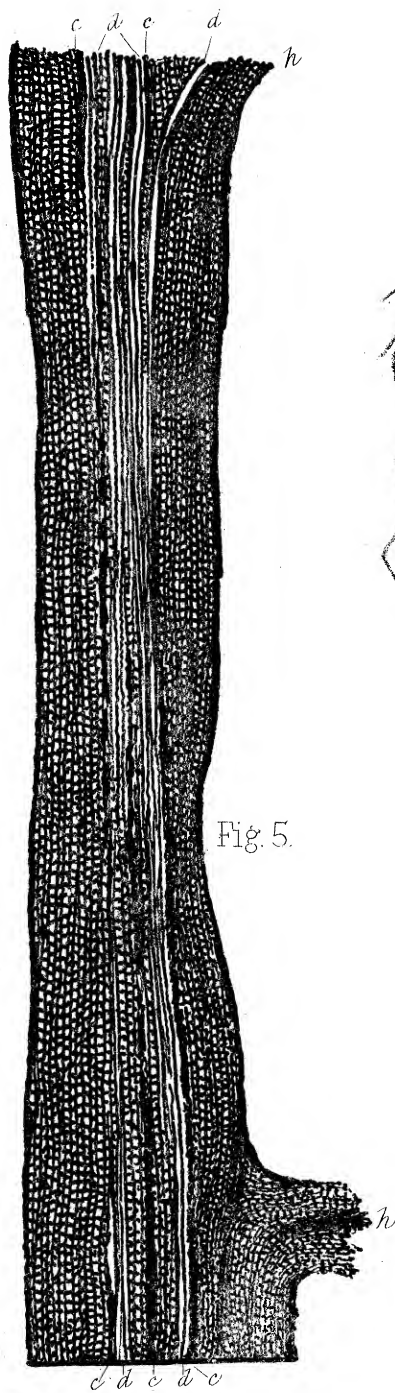
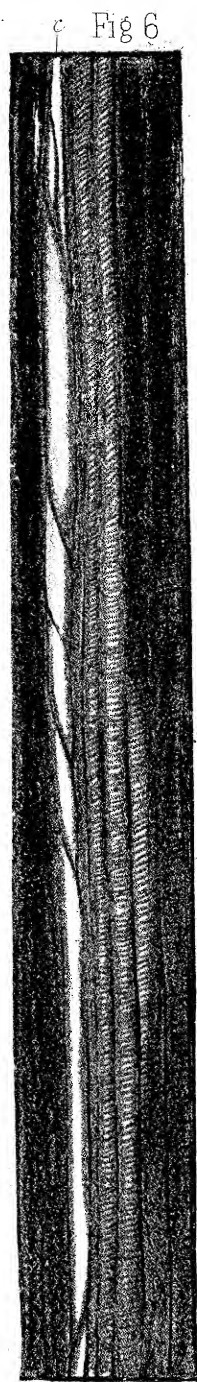
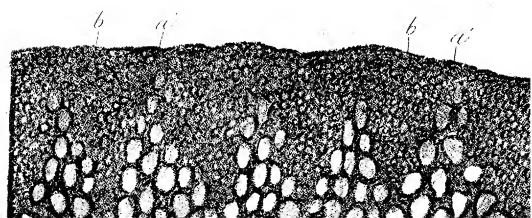
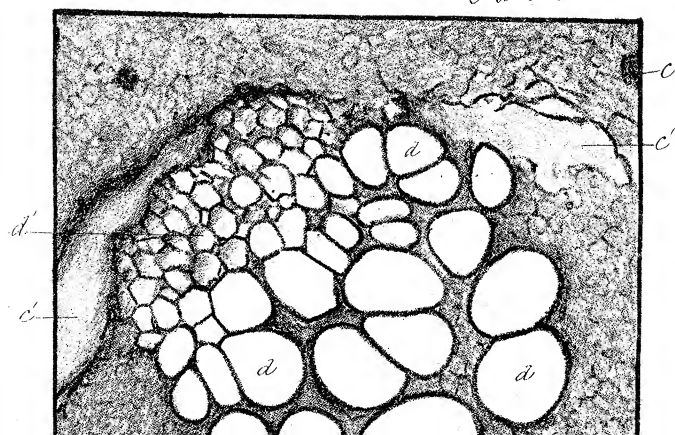
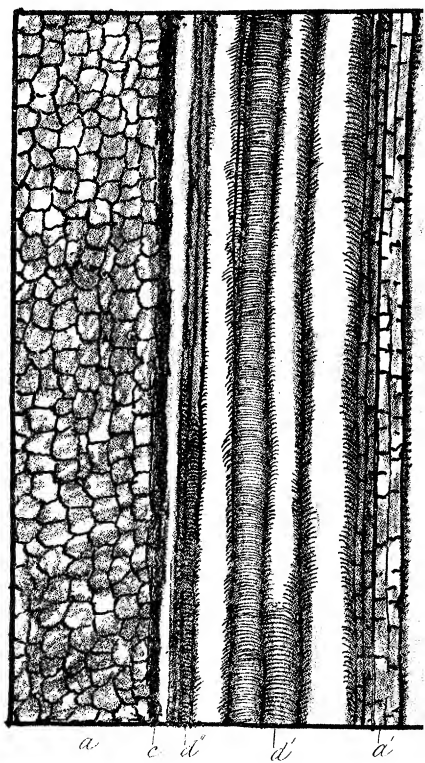
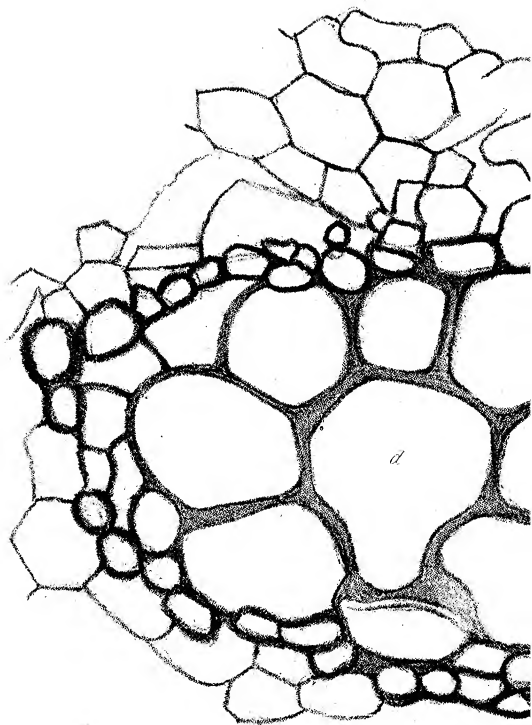


Fig. 5.



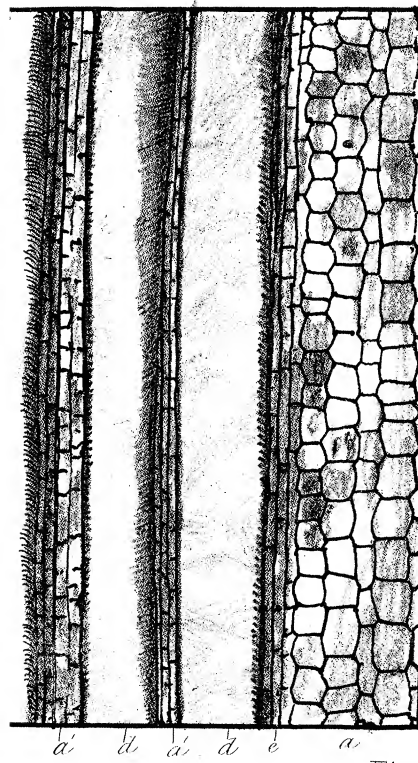
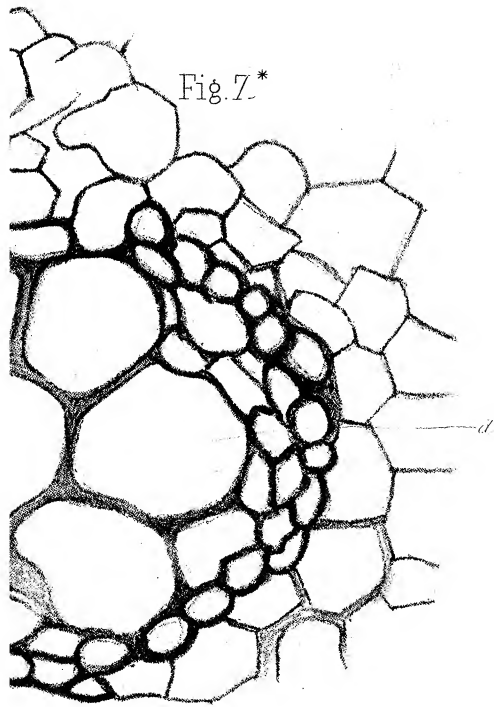
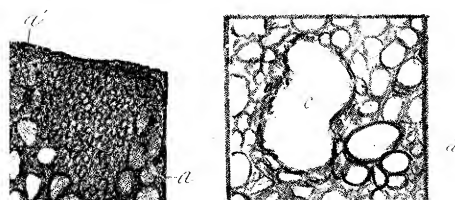


Fig. 8.



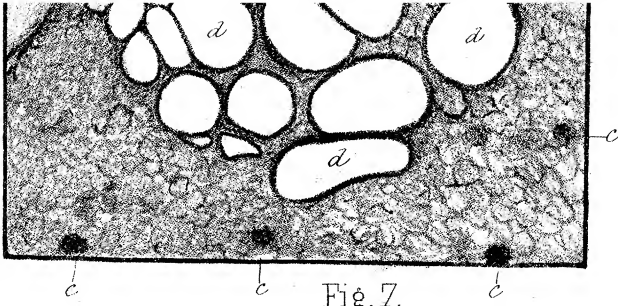


Fig. 7.

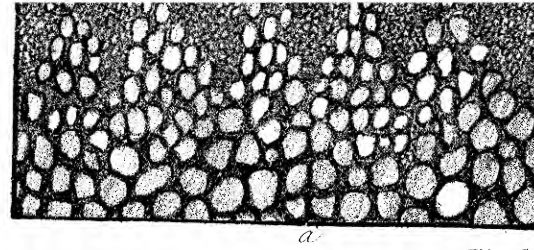


Fig. 1

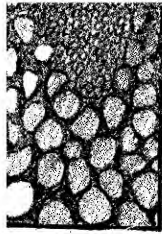


Fig. 16.

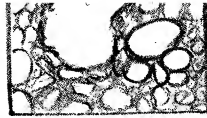


Fig. 11.

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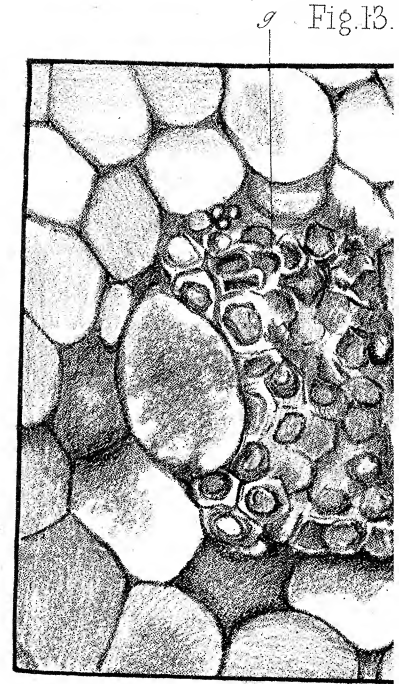
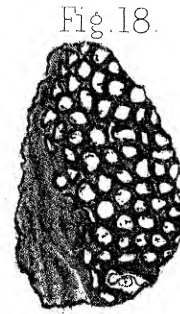
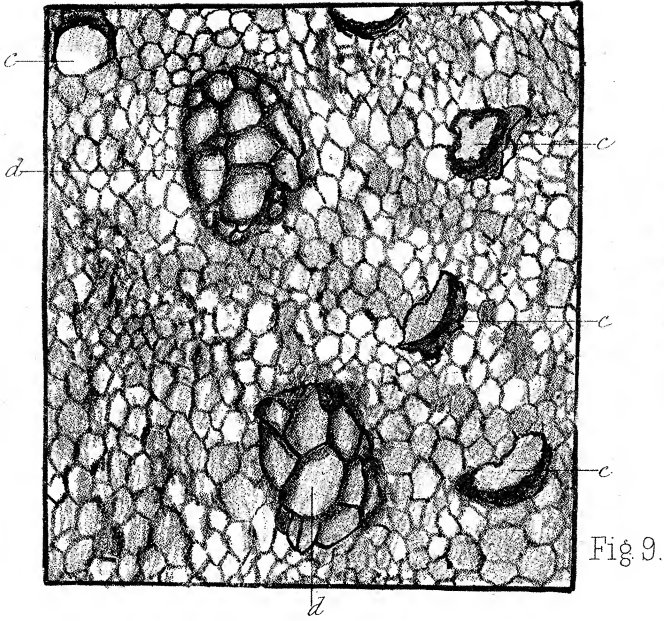


Fig. 15.

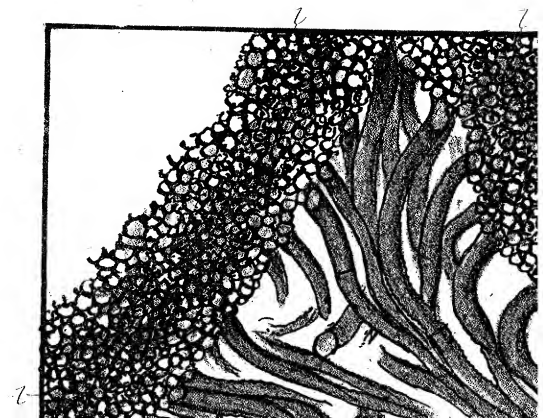
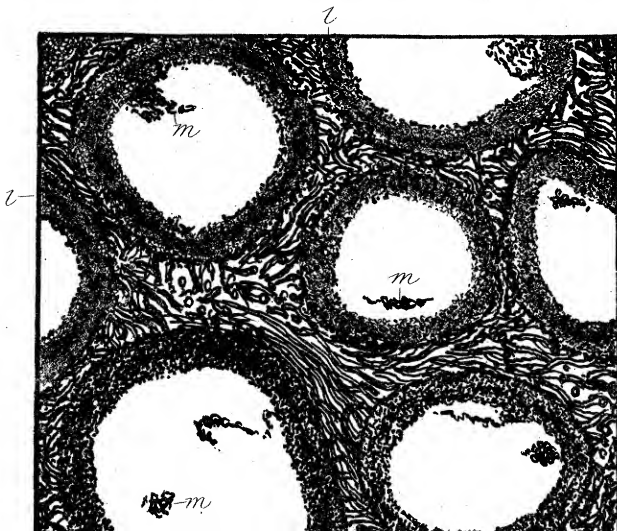
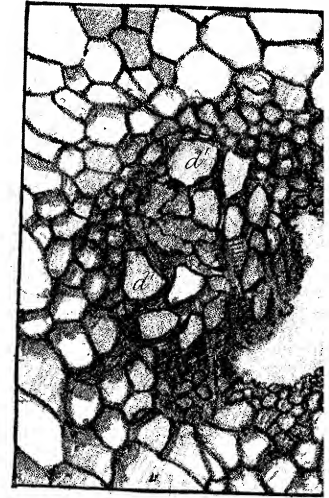
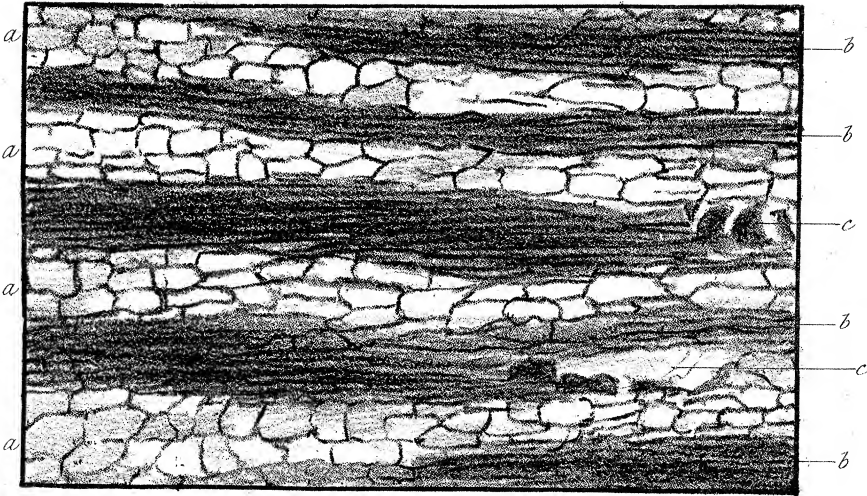


Fig. 13.

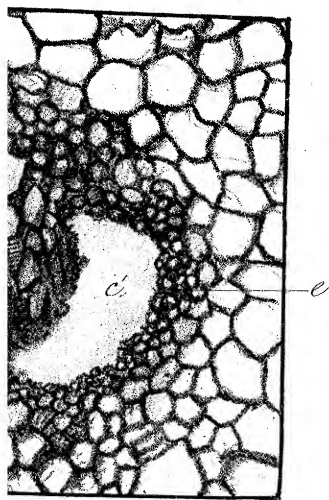
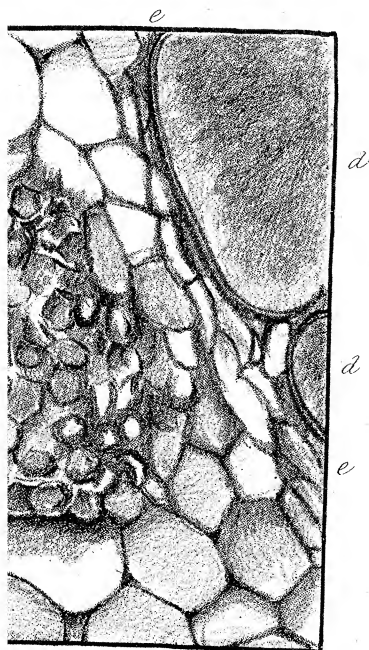
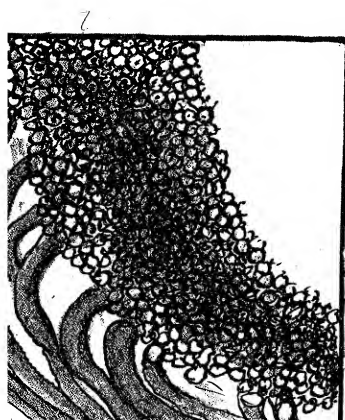
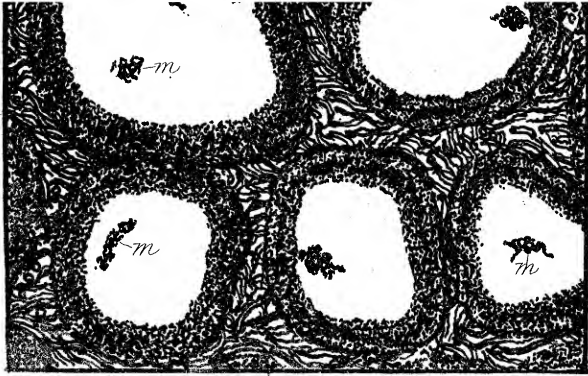


Fig. 14.

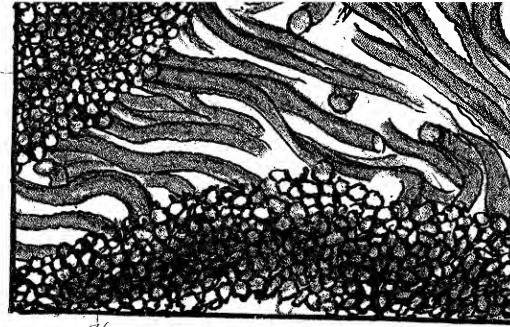




7

h

Fig 20



h

h



Fig 21.

Fig. 29.

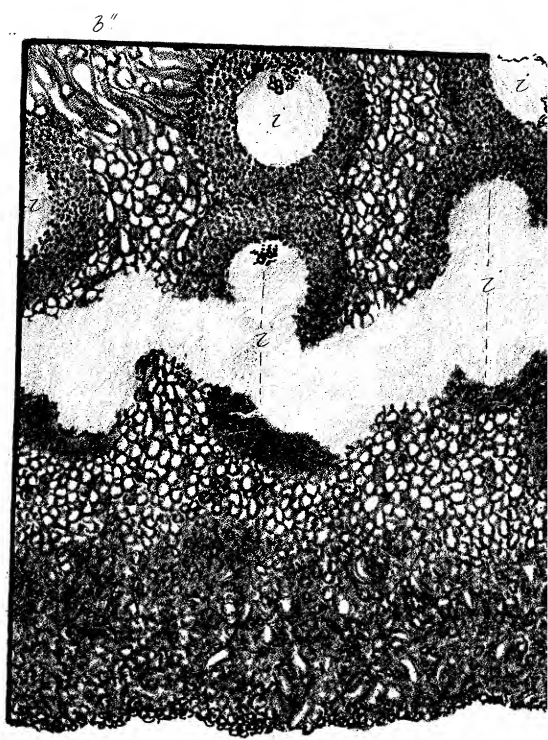
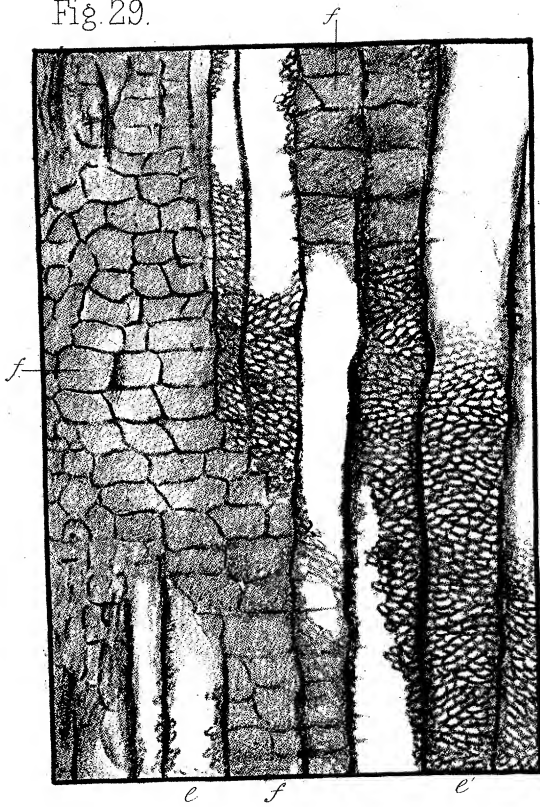


Fig. 17.

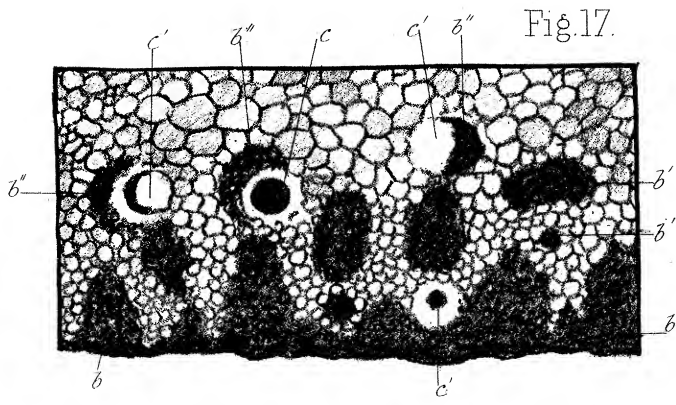
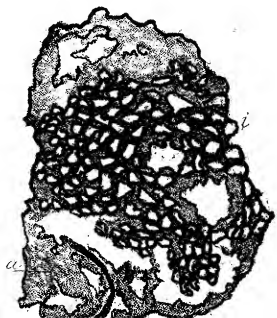
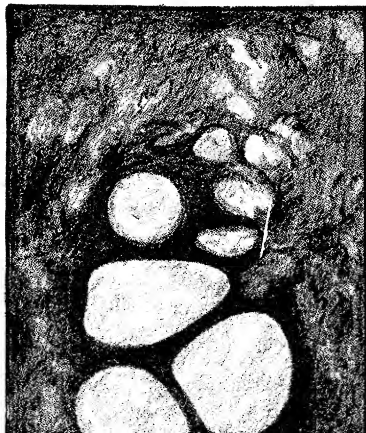
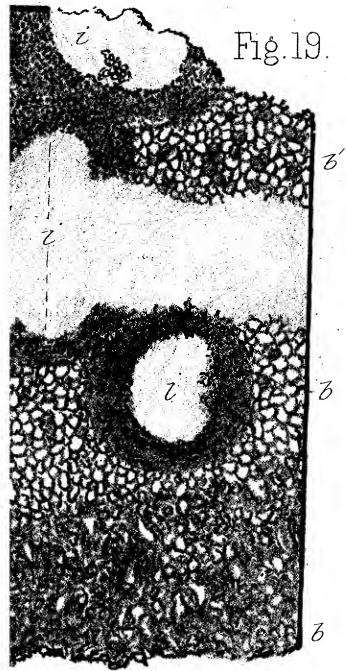


Fig. 22.





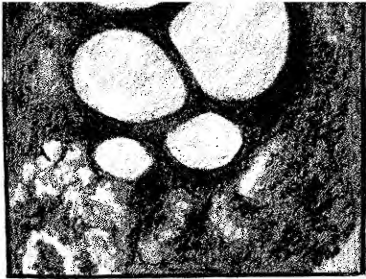
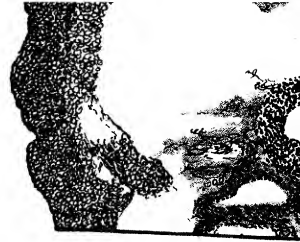


Fig.22 \*



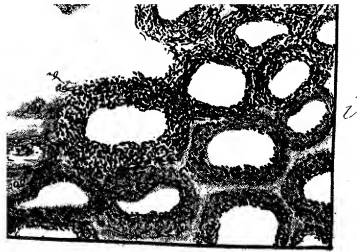


Fig.22.\*\*

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Fig. 23.

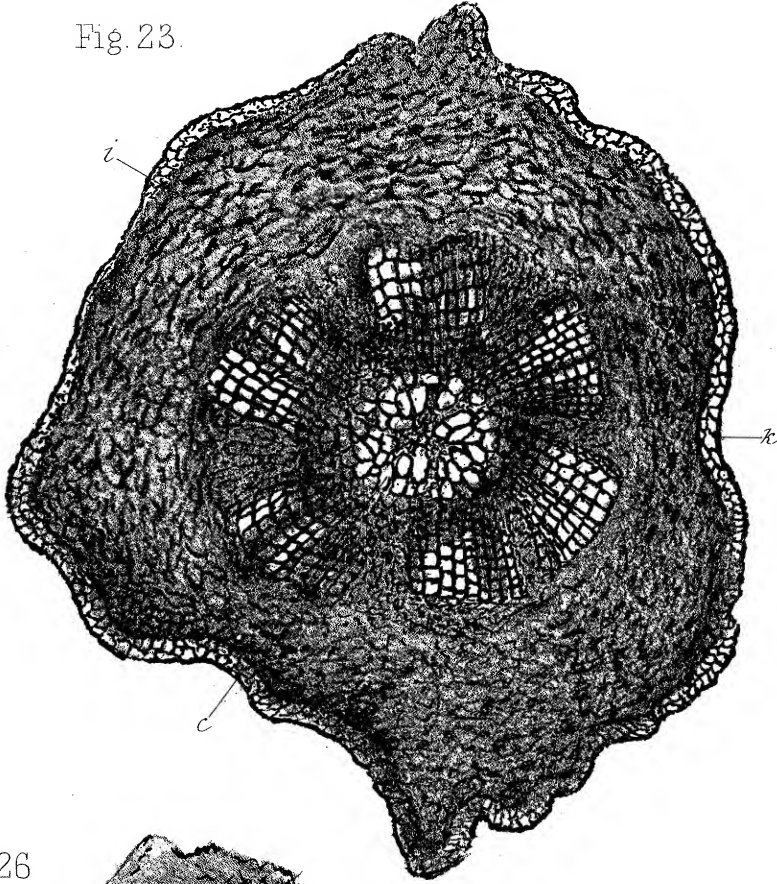


Fig. 26

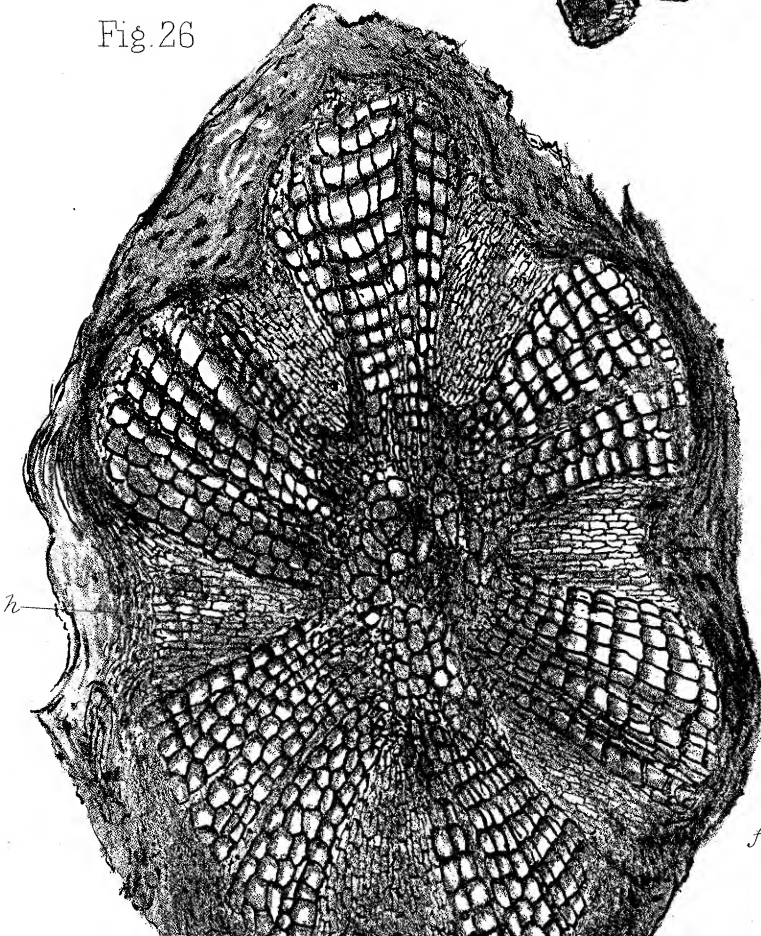


Fig. 25.

Fig. 27.

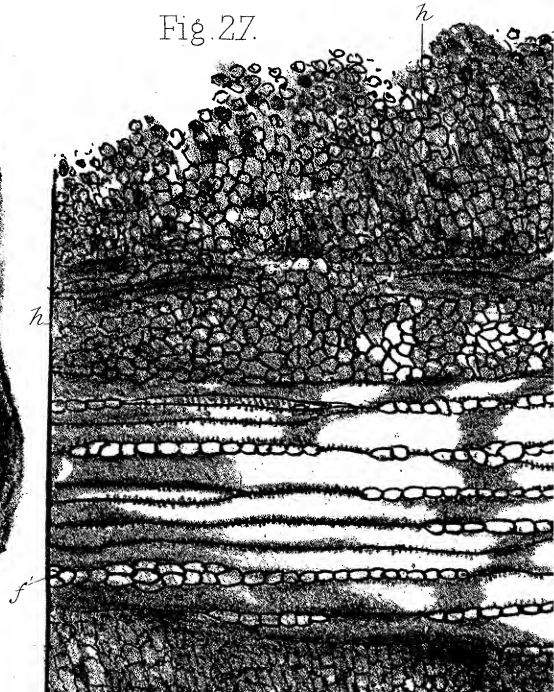
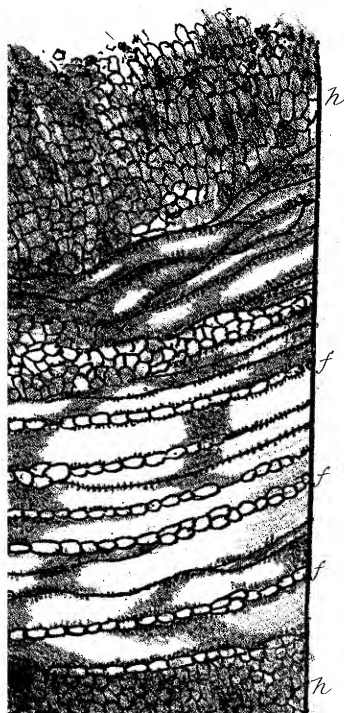
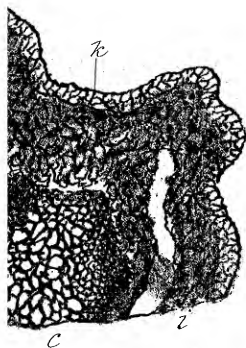
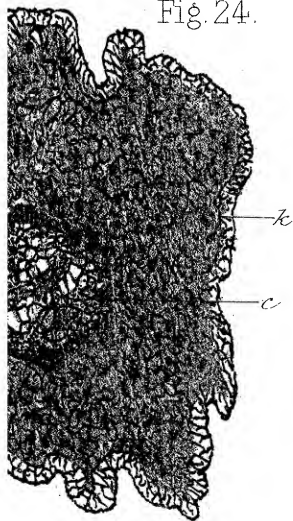
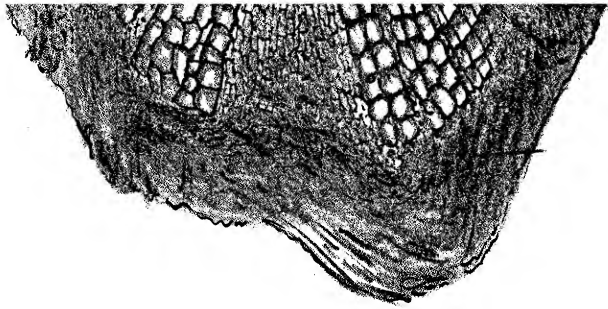
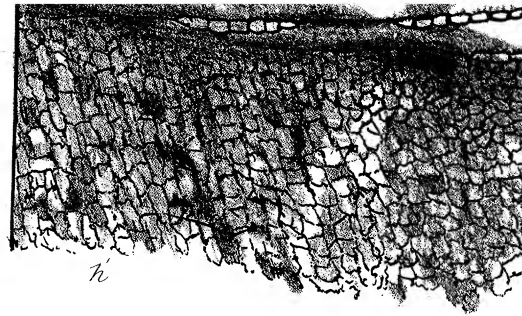


Fig. 24.

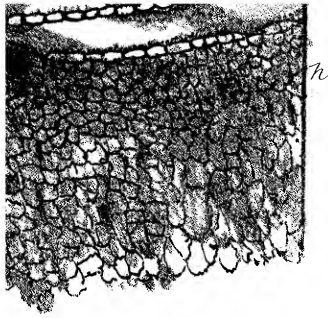




W.C. Williamson, Auto. Lith.



Machu



Machure & Macdonald, Lith. London.

Fig. 30.

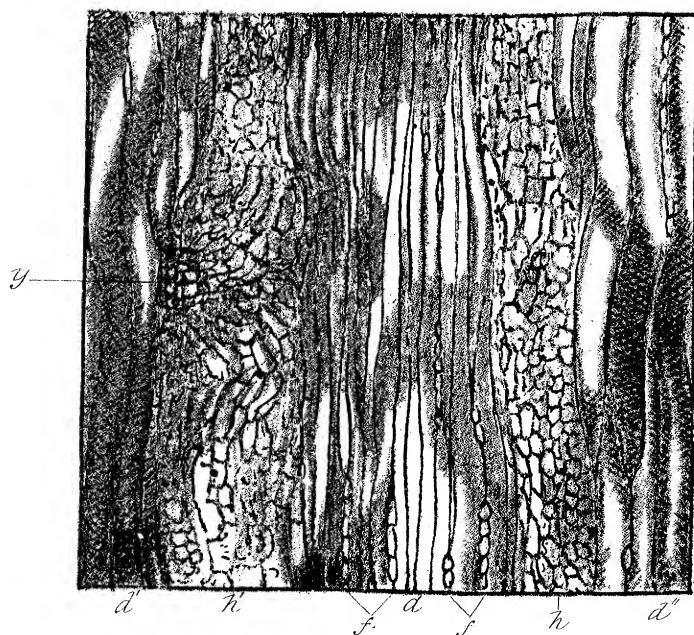


Fig. 31.

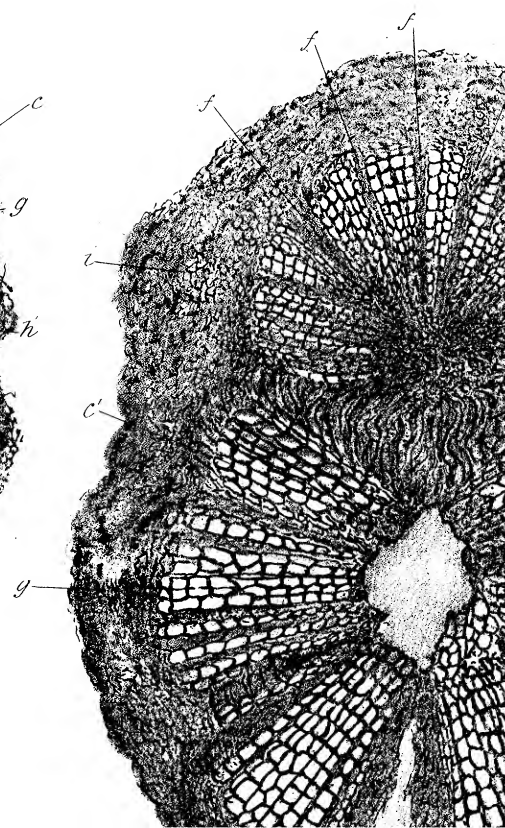
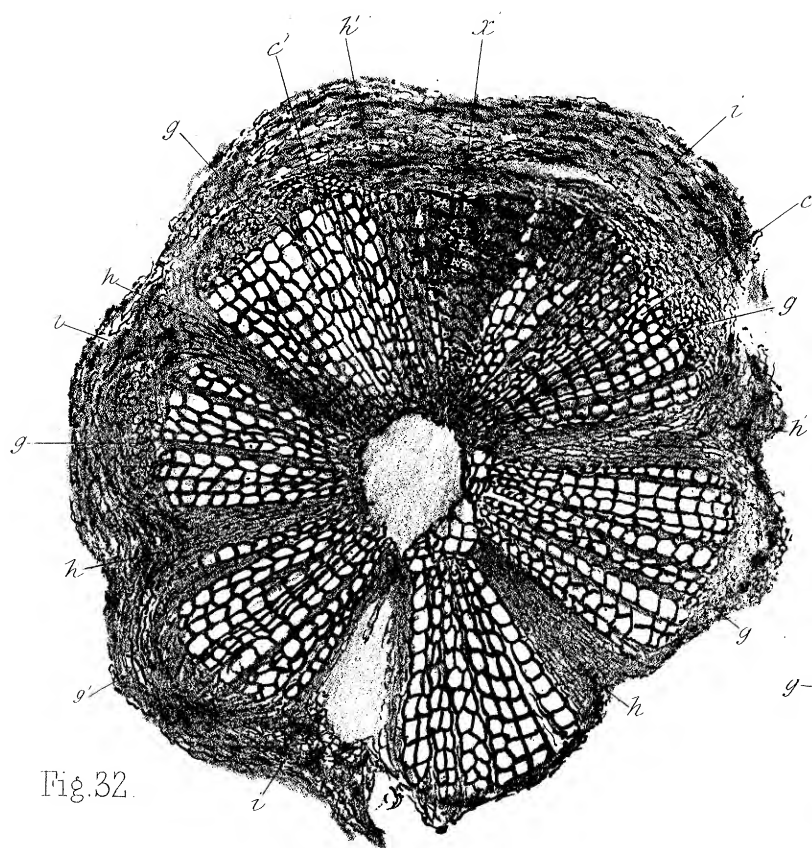
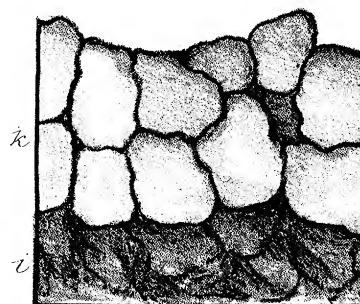
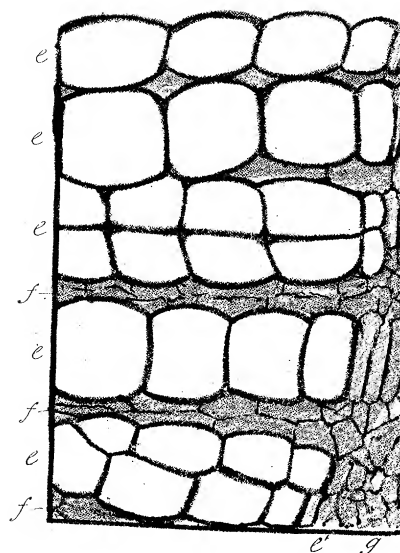


Fig. 32.

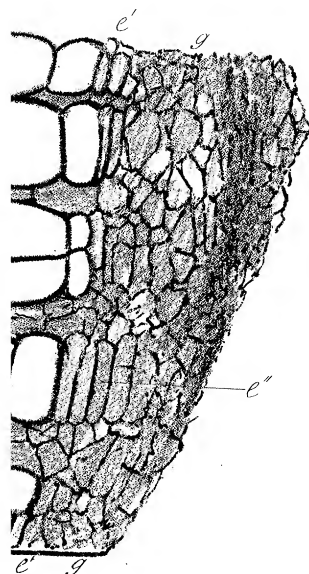


Fig. 28

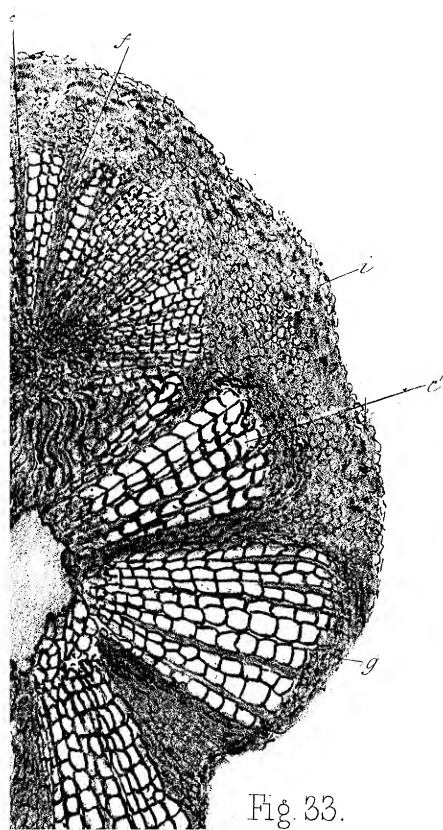
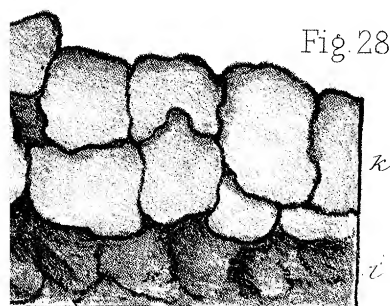
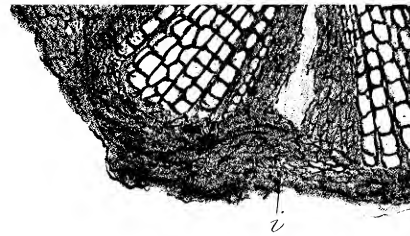


Fig. 33.



W. C. WATKINS

ALBANY, N. Y.

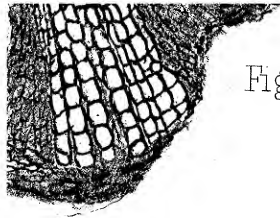


Fig 33.

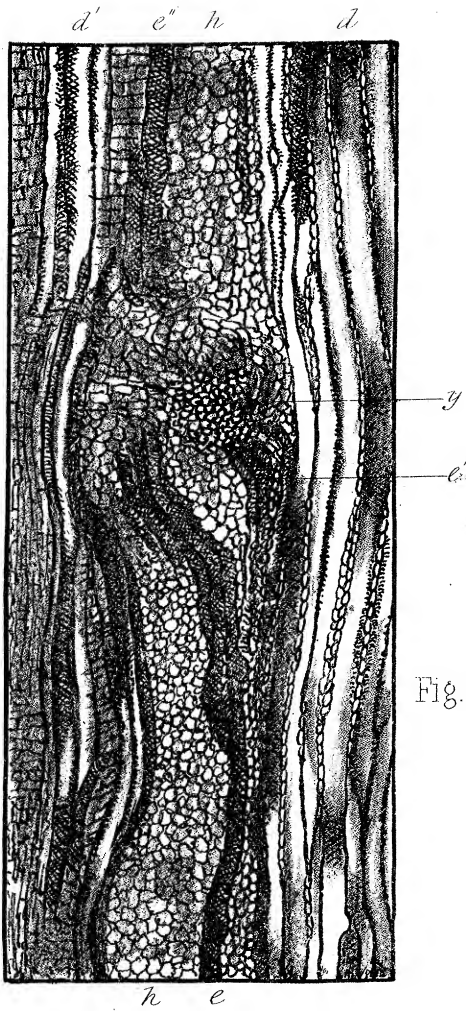


Fig. 35.



Fig. 36.

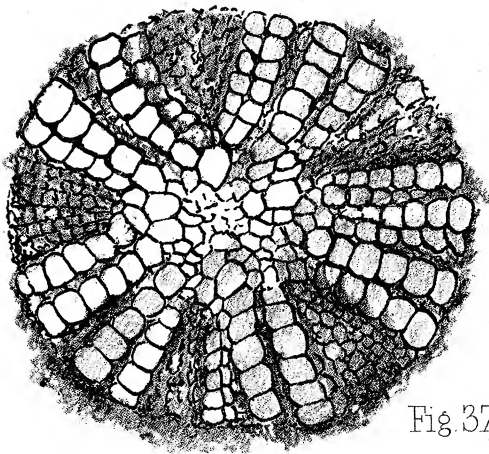


Fig. 37.

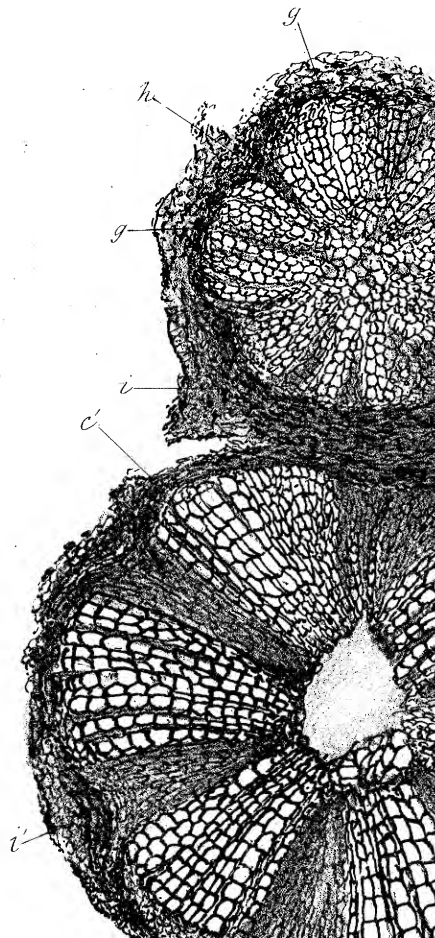
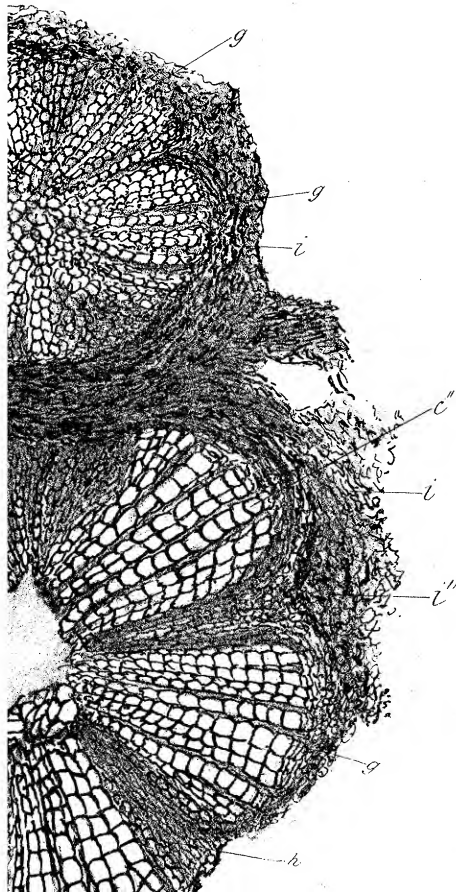




fig. 36.



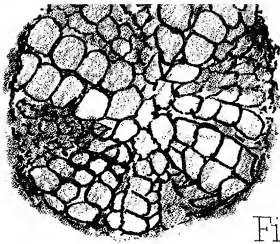
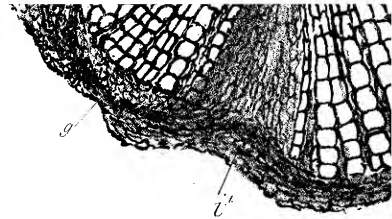


Fig.38.



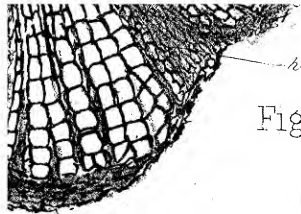


Fig. 34.

Maclure & Macdonald, Lith. London.

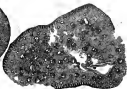


Fig. 4

Fig. 16

Fig. 18

Fig. 1

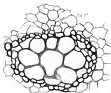


Fig. 2



Fig. 3



Fig. 4



Fig. 5



Fig. 6



Fig. 1



Fig. 2

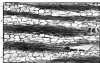


Fig. 4



Fig. 6

Fig. 16



Fig. 19



Fig. 17









Fig. 2



Fig. 3



Fig. 4



Fig. 5